The evolution of large brains and advanced cognitive abilities in animals

Thesis submitted in accordance with the requirements of the University of Liverpool for the degree of Doctor of Philosophy by Christopher Mitchell.

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Preface

This thesis is the product of my own work. The text does not exceed 100,000 words and the document meets the formatting guidelines of the University of Liverpool. No part of this thesis has been submitted to another university in application of a higher degree.

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Abstract

This thesis uses modern, phylogenetically informed statistical methods to conduct four comparative studies aiming to advance the understanding of the evolution of large brains and complex cognition in animals. I begin by reviewing the current state of knowledge about brain size and cognitive ability across a taxonomically broad selection of animals (Chapter 1). I also review the historical approaches to the study of cognition in animals which have informed the current consensus views in different taxa. In chapter two I focus on the comparative method and how the development of phylogenetically controlled statistical methods have influenced the field. I detail the methods used in each subsequent chapter as well as providing detailed methodologies for data collection to help ensure the quality of the data used. In chapter three I use behavioural indicators of advanced cognition in primates rather than using relative brain size. These data show that the evolution of advanced cognitive abilities is strongly correlated with the ecological shift from arboreal to terrestrial niches and not the transition form solitary to social living as expected under the social brain hypothesis. Chapter four addresses a longstanding controversy in cetacean brain evolution by gathering data on cetacean brain size and sociality to compare the social brain hypothesis to the thermogenesis hypothesis. Using the newly developed method of phylogenetic path analysis, I show that the controversial thermogenesis hypothesis is partially supported alongside the social brain hypothesis and I offer a third, competing hypothesis to advance the debate over ceatcean brain size evolution. In chapter five I use large scale comparative data to assess the influence of the host-parasite coevolutionary arms race in birds on the evolution of host cognitive abilities. Against expectations, I find no difference in brain size between hosts of brood parasites and non-hosts. Finally in chapter six, I demonstrate the application of statistical methods to study convergence, such as SURFACE and the Wheatsheaf index, to the study of large brains and cognition in terrestrial carnivores. I argue that quantification of the strength of convergence is an important way forward in

understanding the different forces that have shaped brain size evolution in many different taxa. I conclude with some remarks on the directions for future research. As a whole, this thesis adds to the current state of knowledge on cognitive evolution in primates, cetaceans, terrestrial carnivores and birds as well as raising new questions that future research should aim to address.

1 Introduction

1.1 Abstract

Humans place great significance in intellectual abilities and because of this, biologists have been interested in the cognitive abilities of animals since Aristotle. The difficulties in defining intelligence in a way that can be applied to taxonomically distant animals have resulted in most studies using relative brain size as a directly measurable metric of intelligence. This approach has received criticism but persists in the literature as it has proved to be informative despite imperfections. Large brain size and, by inference, arguably complex cognition have evolved independently in several lineages including primates, corvids, cetaceans, cephalopods and hymenopteran insects. In these varying taxa, the evolutionary history of intelligence is still hotly debated. Proponents of the social intelligence/social brain hypotheses suggest that the cognitive challenges/costs of group living have driven the evolution of large brains whereas other researchers have suggested ecological drivers such as seasonal challenges, dietary differences and energetic constraints. Here I review the study of the evolution of intelligence with particular focus on the widely cited social intelligence hypothesis and cognitive buffering hypothesis. I begin by summarizing the study of animal intelligence and the methods employed. I will then go on to briefly review the current state of knowledge concerning cognitive evolution in some of the most heavily studied taxa. Finally, I will summarize and evaluate the social intelligence hypothesis and the cognitive buffering hypothesis. I propose that the weight of evidence suggests that social intelligence is limited to relatively few taxa, such as primates and cetaceans, and that across other taxa, a variety of other factors have driven the evolution of advanced intelligence in animals.

1.2 Defining and studying intelligence in animals

Intelligence is defined in humans as an individual's performance on a variety of cognitive tasks, often compiled into a metric such as the intelligence quotient (IQ). Researchers investigating animal intelligence are addressing a slightly different phenomenon than IQ by trying to assess species typical intelligence. Most definitions of intelligence employed in the study of animals are similar in that they emphasise the importance of behavioural flexibility and problem solving abilities (Roth 2015). Dicke and Roth (2016) define intelligence as *the ability of an organism to solve problems occurring in its natural and social environment, culminating in the appearance of novel solutions that are not part of the animal's normal repertoire*. This definition has the advantage that intellectual abilities of animals will be observable in the wild and, if tests can be designed that can be applied to a wide variety of species, testable under laboratory conditions.

In order to study intelligence in animals comparatively, a metric that can be applied across taxa is necessary. The most obvious and easily measurable potential index of intelligence is brain size. Absolute brain size is broadly considered not to be a reliable indicator of cognitive ability as most of the variation in brain mass can be attributed to variation in body mass. However, a recent study in which over 500 individuals from 36 species ranging from pigeons to chimpanzees were tested on problem solving tasks that required self-control showed that absolute brain size is the best predictor of performance on the tasks (MacLean et al. 2014) raising the possibility that absolute brain size may be informative. The majority of researchers prefer to consider measures of brain size independent of body size and thus attempt to control for the confounding effect of body size on brain size statistically. The vast majority of studies on brain size and intelligence use either encephalisation quotient (EQ) or residual brain size. EQ uses the allometric relationship between body size and brain size to derive a relative measure of brain size (Jerison 1973). EQ relies on accurately determining the nature of the allometric relationship between brain and body size. Studies of mammals have variously

placed the exponent of this relationship (the slope of the line on a log-log plot of body mass and brain mass) at 0.67 and 0.75 (Boddy et al. 2012). A demonstration of this variation is plotted in Figure 1.1 which shows the differences in scaling relationships of body and brain size between five mammalian orders. Variation in the scaling relationship between body and brain size between groups can be problematic. In a study of cetacean brain size Manger (2006) used the scaling parameter of all mammals to calculate EQs for cetaceans. In fact cetacean brain mass scales quite differently to terrestrial mammals, having a scaling parameter of 0.376 (Manger 2006), possibly due to their aquatic lifestyles (Marino 1998). Improper use of EQs in this manner can drastically alter the results of subsequent statistical analysis as was pointed out in this case by Marino (2008) who advocates the use of relative brain size instead.

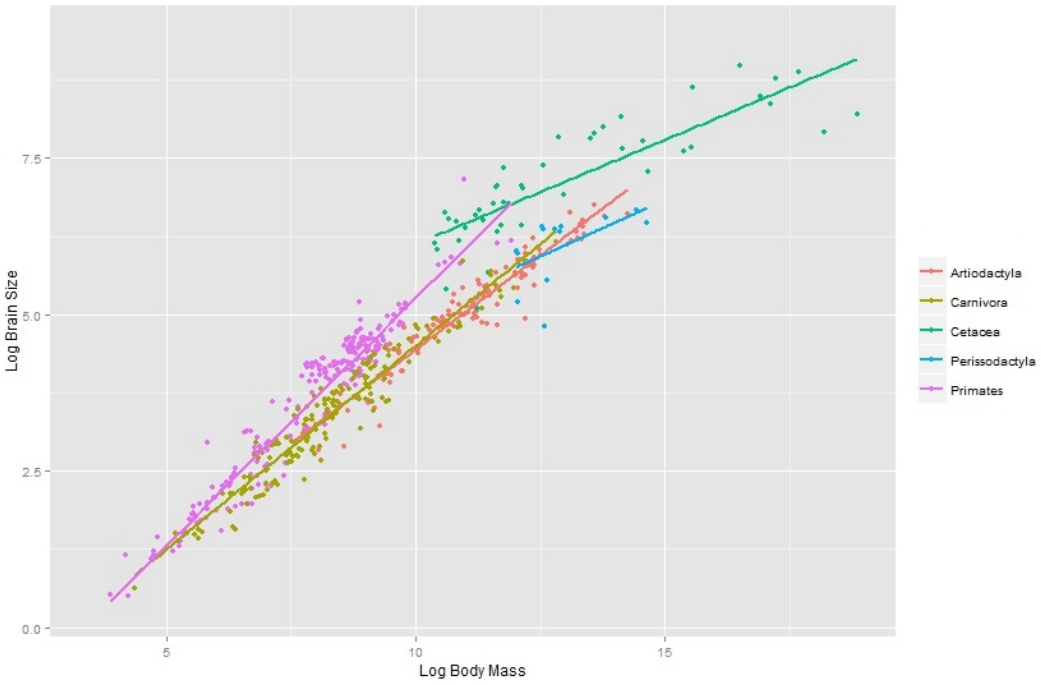

Figure 1.1: Plot of brain and body size across five different mammalian orders showing the differences in scaling relationships between primates, carnivores, cetaceans, artiodactys and perissodactyls.

Using relative brain size is a slightly different methodology. Relative brain size takes account of the correlation between brain and body size in statistical models

and allows researchers to identify any effects down to variation in brain size, independent of body size. There is a vast literature using relative brain size as indicative of intelligence (Healy and Rowe 2007) but this is not without criticisms. Studying brain size as a metric of cognition assumes that any increase in size results in an increase in function or complexity and increases in relative size of specific brain regions may not be detectable by changes in whole brain size (Healy and Rowe 2007).

Some authors prefer to emphasise behavioural flexibility and thus use reported incidences of cognitively advanced behaviours as a quantitative measure of intelligence (Ducatez et al. 2015, Lefebvre et al. 2004, Reader and Laland 2002). For primates and birds, the behavioural ecology literature contains many examples of innovative behaviour because both groups are well studied and researchers are inclined to report their observations. As a result, primate intelligence has been studied using the reported incidences of innovation, tool use, social learning, extractive foraging and tactical deception (Reader et al. 2011, Reader and Laland 2002, Byrne and Corp 2004), and bird intelligence has been studied using foraging and technical innovations (Ducatez et al. 2015, Overington et al. 2009). Similar observations of apparently cognitively complex behaviours from other groups are sparse. In cetaceans for example, there are numerous behavioural observations of a small number of well-studied species but not enough to allow large scale comparative analysis. This approach focuses on behaviour and in doing so, addresses some of the concerns of Healy and Rowe (2007). Most significantly, this approach attempts to study intelligence directly by using complex behaviour as a direct consequence of cognitive complexity and therefore circumvents issues concerning the use of indirect measures such as brain size. Nevertheless, using reports of complex behaviours may be biased towards well studied species, potentially overestimating the complexity of species such as chimpanzees and bottlenose dolphins which are heavily studied for their behavioural repertoires. In such cases, it may be appropriate to correct for research effort in much the same way as brain size is

corrected for body size (Reader and Laland 2002).

1.3 Intelligent animals

Non-human primates have attracted the most attention in the study of animal intelligence due to their close relation to humans and their relatively large brains compared to other mammals. Primates are known for their capacity for cultural transmission (Yamamoto et al. 2013), tool use (Ottoni and Izar 2008, Boesch and Boesch 1990), behavioural innovation (Reader and Laland 2002), tactical deception (Byrne and Corp 2004) and potentially theory of mind (the ability to attribute mental states to others) (Tomasello et al. 2003). The complexity of the behavioural repertoire of primates correlates well with residual brain size and this has been used to argue in favour of a general intelligence (Reader et al. 2011).

Amongst birds, two lineages are held up as possessing cognitive abilities comparable to those observed in primates. Corvids (crows, jays and magpies) have been described by researchers as *feathered apes* because of striking similarities in the cognitive abilities of some corvids and those of the great apes (Emery 2006). Parrots are often held up alongside corvids as extremely intelligent birds and are famous for prodigious vocal learning capacities (Emery 2006). Corvids have been shown to make and use tools (Weir et al. 2002), possess precursors of theory of mind (Bugnyar 2011), exhibit analogical reasoning (Smirnova et al. 2015) and casual reasoning (Taylor et al. 2010). Scrub-jays use cognitively complex strategies to protect their caches from thieves (Emery et al. 2004) and some have argued that crows and parrots can solve problems by insight (Pepperberg 2004, Bird and Emery 2009). The similar levels of cognitive complexity of corvids, parrots and primates has been attributed to convergent evolution (Emery and Clayton 2004).

Cetaceans (whales, dolphins and porpoises) possess some of the largest brains of any animal. Despite the common perception that cetaceans are some of the most intelligent non-human animals, researchers are in fact deeply divided on the ques-

tion of cetacean intelligence. Bottlenose dolphins (*Tursiops truncatus*) and killer whales (*Orcinus orca*) in particular are thought to be highly intelligent based on numerous observations in captivity and in the wild of apparently complex behaviours such as male-male alliances similar to those of chimpanzees (Connor 2007), tool use (Krutzen et al. 2014, Smolker et al. 1997) and communication of identity information analogous to names (Janik et al. 2006). Conversely, some authors assert that despite their relatively large brains, claims of advanced cognition in cetacea are overstated (Manger 2013). Roth (2015) describes experiments on dolphin cognition as generating *mixed and often disappointing results* whereas Manger (2013) asserts that the evidence in favour of complex cetacean cognition becomes considerably less impressive when placed within a broader comparative framework as many of the reputedly complex behaviours occur throughout vertebrates and often invertebrates as well. Such critics generate strong responses from cetacean researchers (Marino et al. 2008, Marino, Lori et al. 2007a) who argue that the weight of evidence in favour of complex cognitive abilities in cetaceans is convincing. Controversy over the intellectual status of cetaceans remains unresolved.

Carnivora, a mammalian order containing approximately 300 terrestrial species and around 30 aquatic species (known as pinnipeds), have been quite well studied and as a result, data on brain size are available for most species. As a whole, the behavioural repertoires of wild carnivorans have not been assessed in a similar manner to primates or birds, making inferences concerning their behavioural complexity difficult. However, a recent study of captive carnivores has shown that relative brain size reliably predicts the ability of a carnivoran to solve a novel problem (Benson-Amram et al. 2016). This would seem to indicate that relative brain size is a reliable metric of cognitive ability.

The cephalopods (octopuses, cuttlefish, squid and nautiluses) have remarkably large and complex brains, especially octopuses which possess the largest, most complex brain of any invertebrate (Roth 2015). Octopuses have demonstrated

abilities such as spatial learning and memory (Boal et al. 2000), observational learning (Fiorito and Scotto 1992) and potentially tool use (Finn et al. 2009).

Rarely considered in studies of intelligence, insects are often thought of as cognitively very simple. However, the neural architecture of insects is relatively well known and in particular the structure known as the mushroom body (corpora pedunculata) has been of particular interest. The mushroom body has been shown to play a major role in many of the behavioural markers of complex cognition including associative learning in *Drosophila* (McGuire et al. 2001), spatial memory in cockroaches (Mizunami et al. 1998) and selective attention in *Drosophila* (Xi et al. 2008). Special attention has been given to the apparently structurally complex mushroom bodies of the hymenoptera which are argued to be the seat of complex cognitive behaviours such as spatial orientation and social behaviour (Roth 2015).

1.4 The evolution of brains and cognition

Hypotheses purporting to explain variation in brain size, and hence cognitive complexity, are numerous and have been the subject of much debate in the literature. These competing hypotheses mostly fall into two schools of thought. Ecological theories propose a direct link between cognitive ability and environmental challenges, supposing that given features of the environment favour increased cognitive abilities to deal with the cognitive challenges posed. By contrast, social theories propose that living in large or complex social groups presents cognitive challenges and so selection pressures that favour grouping will also result in increases in cognitive ability. The social and ecological schools of thought differ on one key point. The crux of this debate is which selection pressure is directly responsible for evolutionary increases in cognitive ability.

1.4.1 The social brain hypothesis

The most broadly cited hypothesis for the evolution of large brains is the social intelligence hypothesis, which posits that large brains and intelligence are an adaptation to social living (Humphrey 1976). Living as a group provides numerous benefits to animals such as protection from predators and assistance in rearing offspring. Living in a social group is also thought to present a variety of cognitive challenges such as navigating a hierarchy, keeping track of interactions and cooperative behaviour patterns. The social intelligence hypothesis states that these problems are solved or managed by having a larger brain and more advanced cognitive abilities to allow animals to cope with increased competition for food and matings. The related social brain hypothesis holds that the costs of living in a group are managed through the evolution of a large brain and complex cognitive abilities (Dunbar 1998, Dunbar and Shultz {2017}).

The social intelligence hypothesis was initially developed as an explanation for large brains in primates, many of which live in large complex groups. Social group size is limited in primates by the relative size of the neocortex which is thought to be the part of the brain most involved with complex cognition (Dunbar 1992, Kudo and Dunbar 2001). These primate findings have formed the basis of much of the research into the social brain hypothesis and social intelligence hypothesis. However, similar relationships have not been found to be universal in animals.

Amongst fishes, cichlids have been shown to exhibit cooperative hunting behaviour and other potentially complex social behaviours (Bshary et al. 2002, Roth 2015). In some cases, these behaviours show some resemblance to primates, particularly observations of social learning and traditions in a variety of species (Bshary et al. 2002). Social group size has been linked to brain size in the cichlid species of Lake Tanganyika (Pollen et al. 2007), supporting a social interpretation of brain evolution. Some studies of brain size in cartilaginous fish have found larger, more complex brain structures in social species such as carcharhinid and

sphyrnid sharks (Yopak et al. 2007).

Studies of carnivores have shown that the social African lion (*Panthera leo*) exhibit sex-specific differences in neocortex size that are absent in the solitary cougar (*Puma concolor*) suggesting a link between sociality and brain organisation (Arsznov and Sakai 2012). In support of the social brain hypothesis, Perez-Barberia *et al.* (2007) argued for a tight co-evolutionary relationship between sociality and relative brain size in carnivorans. However, detailed reconstructions of living and extinct lineages of carnivorans reveal no relationship between sociality and brain size throughout the history of Carnivora (Finarelli and Flynn 2009). In fact, Finarelli and Flynn (2009) determined that the relationship between sociality and brain size in carnivores is limited to the Canidae family and removal of this lineage from their analysis invalidates the claims of Perez-Barbeira *et al.* (2007). The consensus holds that across carnivora, social complexity is not a reliable predictor of brain size and, by implication, cognitive ability. Across Carnivora, relatively large brains are also found in musteloids (weasels, martens, badgers and otters), bears and some of the smaller cats, which all share predominantly solitary lifestyles (Finarelli and Flynn 2009).

The Hyaenidae family, containing just four species, presents a fascinating example of possible convergent evolution of social intelligence within primates and carnivores. The hyaenas are very diverse socially with the aardwolf (*Proteles cristata*) being solitary and the spotted hyaena (*Crocuta crocuta*) having large social groups similar to those observed in cercopithecine monkeys (eg. baboons) (Holekamp et al. 2007, 2015). The similarities between spotted hyaena and baboon social complexity are matched by similar degrees of behavioural complexity and problem solving ability between the groups (Holekamp et al. 2015). As would be predicted by the social brain hypothesis, the spotted hyaena has a larger relative brain size than the other, less socially complex hyaena species (Sakai et al. 2011) and this corresponds with captive spotted hyaenas outperforming other hyaena species on puzzle-box tasks (Holekamp et al. 2015). However, the pattern

within Hyaenidae is not generalisable to the rest of the carnivores (Holekamp et al. 2015, Benson-Amram et al. 2016, Holekamp and Benson-Amram 2017) and it has also been argued that even the spotted hyaena relies on relatively simple forms of social learning such as facilitation rather than imitation for example, suggesting that perhaps the spotted hyaena displays a comparatively simple form of social intelligence (Holekamp et al. 2007).

It is important to note that the social intelligence hypothesis and the social brain hypothesis are not directly concerned with group size but rather with the complexity of social living. The complexity of primate groups is a subject of significant study with considerable variety throughout the clade (Kasper and Voelkl 2009) and the underlying assumption that larger social group sizes imply a more complex social lifestyle has been questioned (Bergman and Beehner 2015). Some efforts have been made to study social network dynamics and the results are less clear. Lehmann and Dunbar (2009) used network cohesion and found that in primates with larger neocortex ratios (the size of the neocortex relative to the rest of the brain), females tend to live in fragmented, smaller grooming clans. They also found that removal of the central figure in a social network caused the group to collapse, suggesting that highly fragmented social systems, also known as fission-fusion groups, and maintaining social cohesion drove the evolution of advanced intelligence of primates rather than simply the increase in the size of the group.

The assumption that larger social groups are more complex seems to hold within primates but not necessarily when we consider other lineages such as fishes, ungulates and birds which occasionally gather in schools, herds or flocks numbering in the thousands or more. These very large groups are not always complex as individuals will typically not engage in complex interactions. In birds, group size shows no relationship to forebrain size (Beauchamp and Fernandez-Juricic 2004). However, Emery and colleagues (2007) note that birds with long-term pair bonds tend to have the largest brains, possibly supporting the social brain hypothesis.

This, combined with the observation that bird flocks are much less stable than primate groups, suggests that it is the cognitive challenges of forming and maintaining long-term bonds that drove the evolution of cognitive abilities in birds. However, other factors influencing intelligence have also been identified including environmental variability (Sayol et al. 2016), ecological generalism (Overington et al. 2011) and a resident lifestyle as opposed to migrant (Sol et al. 2005).

A wealth of comparative analyses of brain evolution in bats has revealed a complex picture. One such analysis demonstrated that monogamous bat species have the largest brains with polygynous species also having relatively large brains but promiscuous species have relatively small brains (Pitnick et al. 2006). Similar results in birds have been used to argue in favour of the social brain hypothesis (Shultz, S. and Dunbar 2010a) but Pitnick *et al.* (2006) suggest that mate fidelity in bats and high relative brain size are both the product of an evolutionary trade-off between brain size and testes size and thus the correlation between brain size and mating system is a by-product of sexual selection. This scenario presents a possible confounding factor in the study of sociality and brain size and casts doubt on some interpretations of links between mating system and brain size. There is some debate concerning these results as Shultz and Dunbar (2007) assert that in fact, the mating system-brain size relationship is a direct causal relationship and that the correlation between brain size and testes size is a by-product of both traits being closely related to mating system. Similarly equivocal evidence comes from ungulates where gregarious species have been shown to have larger brains (Perez-Barberia and Gordon 2005) but other studies have shown that brain size can be predicted by both mating system and ecological factors such as habitat use (Shultz and Dunbar 2006).

Observations of behavioural complexity in hymenopterans (bees, ants and wasps) could be assumed to support the social brain hypothesis because these animals live in some of the most complex social groupings of all. However, Farris and Schulmeister (2011) tested the social brain hypothesis in hymenopterans and

found that a parasitoid life history rather than a social life history is associated with large, complex mushroom bodies. This leads to their interpretation that the cognitive demands of locating a host drove the enlargement of the mushroom body in this lineage, possibly serving as a pre-adaptation for the subsequent evolution of social living (Farris and Schulmeister 2011).

An extension of the social brain hypothesis is the cultural intelligence hypothesis (Van Schaik and Burkart 2011). Under this hypothesis the selective advantages of social learning, such as the rapid spread of novel solutions between individuals, drive increases in behavioural flexibility and general cognitive ability. Thus non-social cognitive skills such as tool use could be a consequence of general increases in intellectual abilities brought about by social living, particularly the social learning aspect of group living which is the underlying mechanism of culture. Evidence in favour of this hypothesis comes from Reader and colleagues (2011) who used observations of primate behaviour reported in the literature and identified a general intelligence factor with social, ecological and technical intelligence very closely correlated.

The observation that primate intelligence is not modular but instead contains a mix of social and technical skills has also been advanced as evidence against the social brain hypothesis. Based on strong correlations between cerebellum size and extractive foraging and tool use but not group size, Barton (2012) proposes the embodied cognition theory of primate brain evolution. This hypothesis proposes that ecological pressures drove the evolution of complex technical skills in parallel to the established idea that social factors drove evolution of social cognition in the neocortex. However, under this evolutionary scenario, we might expect a degree of modularity in primate cognition with the pre-frontal cortex as the seat of social cognition and the cerebellum as the principal component of technical cognition. This seems to be contradicted by Reader's (2011) general intelligence factor which is closely correlated to the neocortex ratio and includes both extractive foraging and tool use. In fact, the cerebellum has been linked to nest complexity in birds

(Hall et al. 2013) and within mammals, the largest cerebellums relative to body size belong to elephants and odontocetes which are thought to be amongst the most intelligent mammals behind some primates (Maseko et al. 2012), although this is debated (Manger 2013, Hart et al. 2008). Furthermore, in humans and other great apes, the cerebellum contains four times the neurons of the neocortex and has expanded considerably more rapidly than the neocortex in the evolution of the ape lineage (Barton and Venditti 2014). These observations challenge an exclusively social interpretation of primate cognition.

1.4.2 Ecological drivers of the evolution of intelligence

Ecological explanations for large brains and complex cognition are varied and have attributed observed patterns of variation in brain size to many factors. The expensive tissue hypothesis states that brain tissue is metabolically very expensive to maintain and evolutionary changes in diet must occur to allow the expansion of the brain in hominins (Aiello and Wheeler 1995). Studies of diet in primates and small mammals have found that folivores have smaller brains than generalists (Harvey et al. 1980) but further work showed that dietary quality, an index calculated from the relative components of each species' diet, does not account for variation in relative brain size in platyrrhine primates (Allen and Kay 2012). However, recent work in primates shows that brain size is predicted by diet rather than sociality, with frugivorous species having larger brains than folivorous species (DeCasien et al. 2017) seemingly contradicting previous findings. DeCasien and colleagues (2017) use a larger sample of species and modern statistical methods, suggesting their study has greater statistical power than previous snaller studies. However, further investigation is required into potential causal relationships between diet and brain size.

Brain size in phytophagous (plant/seed/fruit eating) bats is larger than in animalivorous (flesh/insect eating) bats (Eisenberg and Wilson 1978) which goes against the expectation that high energy diets are needed to support large brains

(Harvey et al. 1980). The larger brains of phytophagous bats have been argued to be the result of the complexity of the foraging habitat, which for bats foraging in dense vegetation provides much greater sensory challenges (Safi and Dechmann 2005). These findings would suggest a strong influence of ecology more generally, rather than simply the energetics of diets, on the evolution of brain size in bats. Thus, despite the intuitive appeal of the expensive tissue hypothesis, diet alone appears insufficient to explain the variation in brain size.

Melin and colleagues (2014) provide evidence in favour of the hypothesis that seasonality in foraging demands, specifically the seasonal dependence on extractive foraging which requires accessing food embedded within a substrate which may require tool use or planning of behaviour, have selected for increased "sensorimotor" intelligence in primates. Strong seasonal fluctuations in food abundance require the ability to respond flexibly and thus are argued to explain the observed instances of tool use and innovative problem solving in primates. Similarly in birds, Sayol *et al.* (2016) analysed over 1200 species and found that species with larger brains are more likely to occur in seasonally varying habitats, suggesting that larger brains confer a selective advantage in enivironments subsequent to frequent and possibly unpredictable changes.

In cetacea, it has been suggested that the relatively large brains of odontocetes (toothed whales) is closely related to their sensory ecology (Jerison 1986). Odontocete cetaceans all echolocate, as did all known fossil odontocetes but mysticete whales (baleen whales), and other aquatic mammals such as pinnipeds (seals and walruses), do not. The processing demands of echolocation could be argued to explain the high degree of encephalisation observed in odontocetes compared to mysticetes. However, it has been pointed out that other echolocating animals such as bats are not highly encephalised (Marino 2007) and therefore echolocation by itself does not explain the large brains of some cetaceans. Another hypothesis proposes that living in cold water has driven the evolution of large brains in cetaceans and large brains in these species have no relation to cognitive abilities

at all (Manger 2006). The so-called *thermogenesis hypothesis* states that the thermal challenges of living in cold waters can in part be solved by expanding the proportion of thermogenic glial cells in the brain and thus generating more heat from the brain without necessarily increasing cognitive function. This hypothesis has been heavily criticised for the dismissal of cetacean species as not exhibiting advanced cognition despite behavioural observations to the contrary (Marino et al. 2008) although these observations are themselves the subject of considerable debate (Manger 2013).

A more general hypothesis is the cognitive buffering hypothesis which proposes that having a large brain gives an organism the ability to respond flexibly in the face of novel, unpredictable challenges posed by the environment (Sol 2009). At first glance, the cognitive buffer hypothesis may appear to be a very broad hypothesis applicable to almost any animal with a large brain in almost any situation. In fact, the hypothesis makes a clear, testable prediction. The key prediction of this hypothesis is that advanced cognitive abilities have significant survival value and this has been shown in birds where the behavioural flexibility of a species predicts the success of invasion (Sol and Lefebvre 2000). Further support for this idea comes from the fact that large brained animals have greater longevity (Gonzalez-Lagos et al. 2010). When presented with a model predator, female guppies (*Poecilia reticulata*) with large brains evaluate the risk and habituate faster than those with small brains (Bijl et al. 2015) suggesting that a general cognitive ability is an important factor in anti-predator behavioural responses. Evidence in support of the cognitive buffer hypothesis can even be found in primates, famed for their social intelligence. A study of catarrhine primates showed that species with large relative brain sizes experienced less seasonality in their dietary intake than species in similarly seasonal habitats with smaller brains suggesting that cognitive buffering allowed these primates to adjust to changing food availability and maintain their energetic intake (Van Woerden et al. 2012).

In marsupial mammals, analysis of brain sizes across the group revealed that

species living in the relatively aseasonal environment of New Guinea have larger brains (Weisbecker et al. 2015). The reduced nutritional pressure on these animals is thought to be a factor allowing the development of large brains. The correlation between brain size and litter size in marsupials (Weisbecker and Goswami 2010) is also taken into account in hypotheses of marsupial brain evolution and leads researchers to conclude that marsupials living in environments with reliable food sources invest more in lactation which allows the brains of the young to grow larger. Crucially, no evidence has been found for any behavioural driving force for the evolution of large brains in marsupials (Weisbecker et al. 2015). This stands in stark contrast to hypotheses which propose that the challenges of certain lifestyles (social living, unpredictable environments etc.) drive the evolution of advanced cognitive abilities to deal with such challenges. Instead, in conditions that allowed large brains to grow, animals that grew large brains, and by inference developed greater intelligence/behavioural flexibility, had a fitness advantage. Weisbecker *et al.* (2015) interpret this as support for the cognitive buffer hypothesis as the general framework for brain evolution in mammals, contradicting claims that the social brain hypothesis should be considered as a general hypothesis for mammals (and birds) (Dunbar 2009). These findings do not necessarily contradict the social brain hypothesis in other groups such as primates but merely demonstrate that the patterns observed in primates and birds is not universal.

1.5 Conclusion

Studying animal cognition is a difficult task. The consensus of many studies is that despite well-known problems and pitfalls, variation in relative brain size does predict performance on cognitive tasks. Therefore, considerable gains in knowledge can be attained from studying brain size. However, it should be noted that taking residual brain size as a measure of cognitive ability is clearly a flawed approach as whole brain size will also correlate with sensory processing abilities

and other non-cognitive tasks. This leads to the conclusion that component parts of the brain may be a more promising avenue of research. This approach has been used very successfully in some groups but can make comparisons between distantly related groups difficult, especially when analogous brain structures may be difficult to identify.

The evidence suggesting that brain size and sociality are causally related, once considered strong and taxonomically widespread, appears to have been weakened by recent research. Although sociality has been strongly linked to cognition in primates and perhaps cetaceans, across mammals there is mixed support for the social brain hypothesis. Uncertainty around the interpretations of different lines of evidence could be resolved by using a reliable measure of social complexity that can be generalised across species such as the number of relationships in a social network. Nevertheless, studies in carnivores, marsupials, bats and social insects have failed to support the social intelligence hypothesis suggesting that the relationship between group living and cognition may be limited to certain clades.

The cognitive buffering hypothesis provides a good paradigm in which to consider the evolution of intelligence. Under this paradigm, if there is a survival advantage to having a large brain and complex cognitive abilities, then we will observe greater survival, longevity, invasion success and adaptation to shifting climates in large brained species. Some studies of birds and mammals have found such patterns as reviewed here and elsewhere. Although the cognitive buffering hypothesis gives an excellent description of how we expect large brains to evolve in circumstances where there are survival advantages, it does not propose a specific factor that may drive the evolution of large brains. This feature of the cognitive buffer hypothesis leaves open the possibility that different factors may have favoured the evolution of advanced cognitive abilities in different lineages. Therefore, the cognitive buffering hypothesis does not stand directly opposed to the social brain hypothesis. Rather, it provides a framework that can be applied

across animals to understand the multiple convergent evolutions of large brains and intelligence.

2 The comparative method in the study of animal cognition.

2.1 Abstract

Here I present a brief overview of the comparative method and in particular, the methodological concerns that surround the recent expansion of comparative studies. I also detail the phylogenetically informed statistical methodologies employed in subsequent chapters as well as the data collection procedures used to assemble large comparative datasets.

2.2 The comparative method

The comparative method in evolutionary biology involves making comparisons between species or populations in order to identify patterns and relationships between traits of interest. This is a powerful method that gives researchers the framework to ask large-scale questions about evolutionary patterns, adaptive processes and coevolutionary relationships.

At its most basic, the comparative method involves comparing one species or lineage to another, or several others, in order to understand how the study group fits into the larger picture of evolution. For example, when a new fossil is discovered it is identified as either a member of an existing species or a new species by comparison to other known fossils. The discovery of *Ardipithecus ramidus* created a great deal of interest when it was discovered because comparison to *Australopithecus* fossils showed that *A. ramidus* was an early hominid species with some characteristics of later species (White et al. 1994, Leakey et al. 1995). As more data became available with subsequent fossil finds, the place of *A. ramidus* in hominid evolution became clearer, giving insights into the evolutionary processes and patterns in the whole hominid clade (White et al. 2009, Suwa et al. 2009, Lovejoy 2009).

In the study of cognitive evolution, most claims of convergent evolution in brain size and/or cognitive complexity arise from descriptive comparisons of two or more taxa. Comparison of corvid and parrot brain size and behaviour have resulted in claims of convergence with great apes in terms of their cognitive abilities (Emery and Clayton 2004, Emery 2006) and a similar comparative methodology has identified possible convergence in social intelligence between spotted hyaenas and baboons (Holekamp et al. 2007, 2015, Holekamp and Benson-Amram 2017). Roth (2015) applied simple comparison more broadly in his review of the convergent evolution of complex brains and intelligence across all animals to discuss the varying selection pressures that may have ddriven the evolution of different

cognitive abilities in different groups.

Another kind of comparative study takes data gathered from many species and searches for patterns and relationships within the group. Studies of this nature rely on a great deal of work done by others, often totalling many lifetimes worth of primary research into individual species. Reader and colleagues (2011) carried out an extensive literature search looking for examples of five behavioural traits in many species of primate in over 4000 articles published over 75 years. The resulting database included examples of innovation, social learning, tool use, extractive foraging and tactical deception and was used to demonstrate a correlation between these behaviours and brain size, providing evidence of a general intelligence factor in primates similar to that in humans (Reader et al. 2011).

Analyses of this kind must deal with the fact that each data point in the sample is not statistically independent (Nunn 2011). This is because each species is a product of evolution and related to every other species by varying degrees. For a trait evolving under simple Brownian motion, two closely related species are highly likely to be phenotypically similar because they share most of their evolutionary history and have only had a comparatively short time to diverge. Similarly, distantly related species are more likely to have widely varying phenotypes because these species have been evolving separately for a much longer time than closely related species. Therefore, we should expect traits to vary in a predictable manner because of the phylogenetic history that connects each datum. The tendency for closely related species to resemble each other rather than any other random species taken from the phylogeny is known as phylogenetic signal (Harvey and Pagel 1991, Blomberg and Garland 2002).

In an analysis of a variety of morphological, behavioural, life history and physiological traits, Blomberg and colleagues (2003) showed that over 90% of traits with a sample size larger than twenty species show significant phylogenetic signal. Different categories of traits tend to have different degrees of phylogenetic signal. For example, morphological traits like body mass tend to have very strong

phylogenetic signals whereas behavioural traits tend to have weaker phylogenetic signals (Blomberg et al. 2003). It could be argued that this is because behavioural traits have much greater measurement errors than morphological traits or perhaps that behavioural traits have much more intraspecific variation or possibly that behavioural traits change more rapidly over evolutionary time, reducing phylogenetic signal as phenotypes across the tree can change relatively quickly producing a pattern closer to a random distribution of traits.

For comparative studies, any patterns or relationships that can be explained by the pattern of relatedness among data points, can potentially obscure the 'true' relationships being studied (Felsenstein 1985). The relatedness of data points may obscure an interesting relationship, resulting in a type II error in which we would fail to reject the null hypothesis of no relationship. Alternatively, and much more commonly, phenotypic similarities due to the statistical non-independence of data points may exaggerate relationships, causing type I errors in which the null hypothesis of no relationship is incorrectly rejected. In fact, type I errors have been shown to be much higher in non-phylogenetically corrected cross-species comparisons (Harvey and Rambaut 1998) compared to similar tests conducted using independent contrasts which corrects for phylogeny by calculating the differences in trait values between closely related pairs of lineages (Felsenstein 1985, Nunn 2011).

In order to control for the potentially confounding effect of shared evolutionary history, statistical analyses must take the phylogeny of the study group into account. Many methods have been developed that use phylogenies in various ways to control for this effect. The methods employed in this thesis will be reviewed in more detail in the 'Methods' section of this chapter. In general, these methods use phylogenetic data to correct the analysis for the statistical non-independence of data points. This can take a variety of forms. In reconstruction based methods, the phylogeny is used as a backbone upon which the history of a trait is mapped over time. Alternatively, in a phylogenetic regression for example, the structure

of the phylogeny is transformed into a covariance matrix and incorporated into the statistical model as an error term (Grafen 1989).

2.3 Comparative data

The development of phylogenetically controlled comparative analysis methods has proceeded rapidly over recent decades and this has resulted in a wealth of comparative studies being published. For example, Healy and Rowe (2007) present a list of 54 comparative studies that have looked for evidence of correlations between brain size and behavioural complexity in mammals and birds alone between 1996 and 2006. The widespread adoption of phylogenetic comparative methods over traditional statistical analyses is encouraging and demonstrates widespread agreement on the need for statistical rigor. Similarly, the expansion of comparative studies has produced a large amount of comparative data covering a great deal of information on a vast number of species.

Having a large amount of data available in the literature enables researchers to study a great many interesting questions. However, the suitability and accuracy of the data is an important issue that is not always fully addressed. Borries and colleagues (2016) detail a number of concerns that researchers should be aware of when assembling comparative databases. For example, it is reasonable to assume that the author(s) of a given comparative study will not always be experts in every species under study and so erroneous data points that might be recognised and discarded by experts in a particular species or trait, may be accepted. Data that has been gathered using different methodologies may not always be comparable or data gathered from a small sample size may not accurately represent a species, casting doubt on the conclusions of a study.

With these concerns over data suitability and accuracy in mind, Borries *et al.* (2016) propose four 'guiding principles' which are designed to improve the quality of comparative data sets. The first of these principles states that researchers

must include explicit definitions for each variable collected and descriptions of the methods used to collect the original data. This will aide not only the interpretation of the study being performed, but also any future researchers using the same data to assess the suitability of the data for their study. The second principle involves including metadata with each datum. This may take the form of details such as sample size or geographic coordinates where each datum was recorded. The third principle holds that researchers gathering together data for a comparative study should thoroughly document the procedures they use to track and locate data. The fourth and final principal to follow is that the data used should be made available in an easy to use, universally accessible format.

Implementing the suggestions of Borries *et al.* (2016) requires a large investment of time at every level from the primary researcher gathering data to the authors and reviewers of comparative studies. Nevertheless, it is important to allay any concerns over the provenance of data in comparative research and so in this spirit, the following section of this chapter is concerned with detailing the methods employed to gather and analyse the data used in the following chapters.

2.4 Methods

2.4.1 Chapter Three: Terrestrial living and the evolution of advanced cognition in Primates.

In Chapter three, I gather social, behavioural and life history data from across primates to examine the evolutionary history of advanced cognitive behaviour. This analysis uses behaviour rather than brain size as a direct metric of advanced cognition. I test for correlated evolution in the development of advanced cognition and ecological and social transitions in primate history. I also evaluate the relative predictive power of social, ecological and life history traits on cognitive evolution.

2.4.1.1 Comparative data

As behavioural indicators of advanced cognitive abilities, data on four behaviours (innovation, social transmission, tool use and extractive foraging) were provided by Reader *et al.* (2011). These data were originally gathered by an extensive literature search using keywords to classify examples of each behaviour. Using keywords such as 'novel' to denote an innovative behaviour means that the original author(s) of the paper describing the behaviour makes the determination of whether a particular example truly represents the category of behaviour. This measure counters concerns that non-expert judgements may bias the data (Borries et al. 2016, Reader et al. 2011). Reader *et al.* (2011) provide definitions for each behaviour. Innovation is defined as the tendency to *'discover novel solutions to environmental or social problems'*. Social learning is defined as the tendency to *'learn skills and acquire information from others'*. Tool use is defined as simply as the ability to *'use tools'* and extractive foraging is defined as the tendency to *'extract concealed or embedded food'*. In my analysis (see Chapter 3), each primate species searched for by Reader *et al.* (2011) is classified as either exhibiting advanced cognition or not depending on the presence or absence of one or more of these four behavioural indicators. I define the new binary variable 'advanced cognition' as *the cognitive complexity required to perform at least one of innovation, social learning, tool use or extractive foraging.* This definition is specific to the study being performed and the connection between advanced cognition, as defined here, and intelligence is supported by the conclusions of Reader *et al.* (2011) who showed that these behaviours are positively related to brain size and are attributable to a single 'general intelligence factor'. More broadly, intelligence is defined as 'the ability of an organism to solve problems occurring in its natural and social environment, culminating in the appearance of novel solutions that are not part of the animal's normal repertoire' (Dicke and Roth 2016). This definition fits well with the advanced cognition classification advanced here.

Searching the literature for data of this nature allows researchers to generate an overview of the entire group under study but can potentially be biased if

research effort is not evenly distributed amongst the study group. In primates, and especially in the case of behavioural and cognitive studies, certain species are much more heavily studied than others, possibly because certain species are easier to study because of geographic distribution or perhaps certain species are considered more interesting and therefore worthy of greater research effort (Hawes et al. 2013). To correct for this potential bias, the standard method is to take the residuals from a log-log regression of the trait in question against an index of research effort (Reader and Laland 2002). Alongside the behavioural data, Reader *et al.* (2011) also provide data on research effort, indexed as the number of articles published on each species of primate in the Zoological Record database. Since using a simple regression as others have done is inappropriate to correct a binary variable for research effort, here I eliminate all species in the database with a research effort less than the lowest research effort amongst species that were classified as exhibiting advanced cognition. This approach makes the assumption that the lowest research effort amongst the species that are positively identified as exhibiting advanced cognitive abilities is sufficient to determine whether a given species truly exhibits the behaviours listed here. In doing so, the aim is to remove any species from the analysis that is not studied in enough detail to be confidently classified as either possessing advanced cognitive abilities or not.

Social group size data were taken from a recently published comparative database, assembled from numerous sources in the literature (DeCasien et al. 2017). From these various sources, DeCasien and colleagues (2017) removed duplicated values, leading to an average of 4.7 data points for each species. From these data the average group size for each species was calculated by the original authors.

Home range size was collated from three sources. The first, entitled PanTHERIA (Jones et al. 2009), defines home range as the *'size of the area within which everyday activities of individuals or groups (of any type) are typically restricted'* and is measured in km^2. Additional data were gathered from two published datasets (Nunn et al. 2004, Nunn and Barton 2000) in which geographic home

range is measured in hectares. These data were converted to km^2 by multiplying the values by 0.01 as there are 100 hectares in 1 km^2.

Diet breadth is defined as the *'number of dietary categories eaten by each species… for non-captive or non-provisioned populations'* (Jones et al. 2009). The categories referenced in the definition are listed in the metadata of PanTHERIA as *vertebrate*, *invertebrate*, *fruit*, *flowers/nectar/pollen*, *leaves/branches/bark*, *seeds*, *grass*, and *roots/tubers*.

Maximum longevity is defined as the *maximum observed adult age* reached by a species (Jones et al. 2009). Data from PanTHERIA (Jones et al. 2009) were gathered on maximum longevity (measured in months). These data were supplemented with data from other comparative databases (Lindenfors 2002, Barton 1999), ensuring in each case that the data is converted to months.

Activity pattern is defined as the *principal period of activity* for each species and can be classified as diurnal (active mostly or entirely during daylight), nocturnal (active mostly or entirely during the night) or cathemeral (irregularly active throughout day and night). Classifications for each species' activity pattern were gathered from 3 published databases (Barton 1999, Kappeler and Heymann 1996, Nunn and Van Schaik 2002).

Finally, species were classified as primarily terrestrial or arboreal based on whether they spend the majority of their time in either habitat (Nunn and Van Schaik 2002).

2.4.1.2 Phylogeny

A species-level primate phylogeny was acquired from the 10ktrees project (Arnold et al. 2010). The 10ktrees primate phylogeny used in this thesis is version 3 of the phylogeny. The authors collected data for eleven mitochondrial and seven autosomal genes across 301 species of primate (Arnold et al. 2010, 2012). Using the aligned sequences of these genes, the authors then inferred the structure of

the phylogeny using Bayesian analyses to produce 10,000 possible trees. The benefit of sampling many trees from a Bayesian inference chain in this manner is that each tree is a plausible representation of the 'true' phylogenetic structure whilst any uncertainty about some features of the tree is preserved. For example, some relationships, nodes and branches will be identical, or very similar, across the entire block of trees and these well supported aspects of the phylogeny are considered fairly certain. Conversely, amongst the tree block, the topologies will differ at points of uncertainty where the relationships between species are less clear from the data provided (Arnold et al. 2010, Nunn 2011, Huelsenbeck et al. 2000). In chapter three, I use the consensus primate phylogeny from the 10ktrees project with branch lengths proportional to time (Arnold et al. 2010). This is a single phylogenetic tree constructed from the block of 1000 trees with branch lengths calculated as the mean of all branch lengths in the tree block (Arnold et al. 2012).

2.4.1.3 Analysis

Many comparative analyses are primarily concerned with identifying correlated evolution between two or more traits and making inferences about the potential causal relationships between traits. Pagel (1994, 2006) developed a method to detect correlated evolutionary change in discrete traits using the structure of the phylogenetic tree to estimate rates of change in each trait through evolutionary time. The method involves fitting two models to the data, which take the form of two binary variables. For two binary traits there are four possible character states a particular species can occupy; 00, 01, 10 or 11. The first model, called the *independent model*, allows for both traits to evolve independently of each other and therefore estimates four parameters. These four parameters describe the rates of change between the four possible states and so according to the independent model, the rate of change of each trait is the same regardless of the state of the other trait. In the second model, changes between the four states are modelled

such that a change in one trait is allowed to be dependent on the condition of the other trait. This means that the rate of change in a trait is estimated once when the other trait is one state, and again when the other trait is in the second state, giving eight parameters in this *dependent model*. A schematic depicting the structure of this analysis is shown in Figure 2.1.

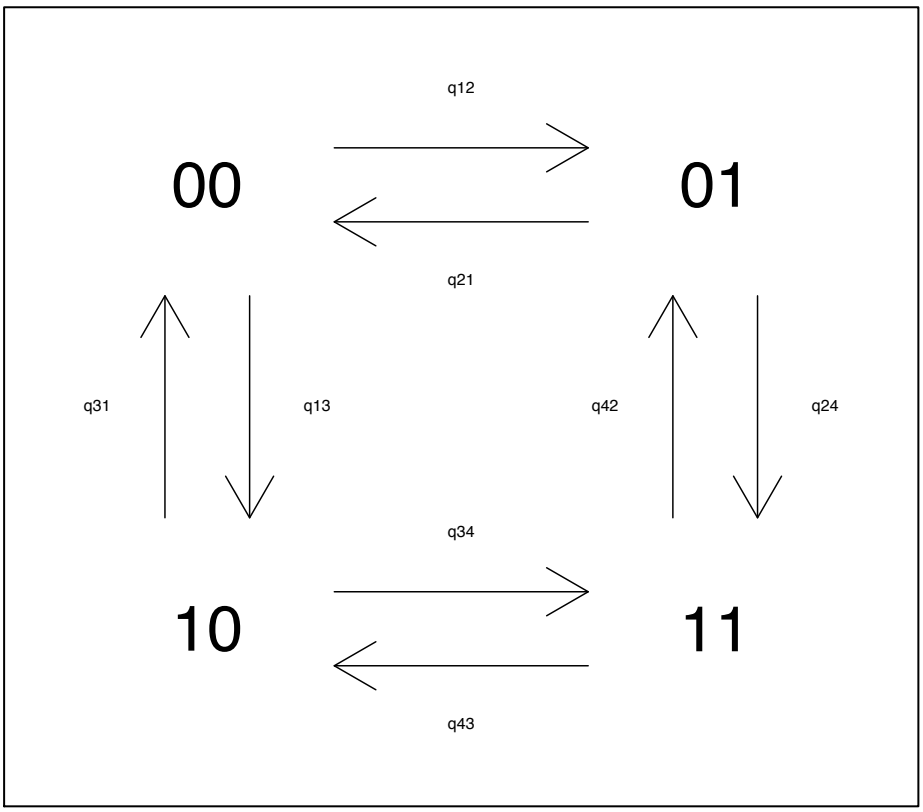

Figure 2.1: Diagram depicting the eight transitions between four states possible with two binary characters. Transition labels refer to the changes between states in the order listed in the text. For example, q12 refers to the transition between state 1 (00) and state 2 (01). Reproduced from Pagel and Meade (2006)

The log likelihoods of the dependent and independent models are compared using a likelihood ratio test with degrees of freedom equal to difference in the number of parameters in the models. If the dependent model is a significantly better fit to the data than the independent model, this is taken as evidence of correlated evolution between the two traits under study. Once correlated evolution has been established, further constraints can be placed upon the model to test specific hypotheses, allowing causal hypotheses to be tested. For example, a specific

transition can be constrained to occur at equal rates, such as the gain of one of the traits being studied. This seven parameter, constrained model can then be compared to the unconstrained, dependent model using a likelihood ratio test. In this way, the magnitude and direction of the influence of the second trait can be determined. If the constrained model is a better fit to the data, then the second trait does not significantly affect the rate of change in the first trait. In this way, it can be determined if rates of change in the first trait are higher when the other trait has a particular value and thus, whether one trait influences the evolution of another in a particular direction. In Chapter three, I use these methods developed by Pagel (1994) to test for traits that coevolve with advanced cognition. The analyses were performed by using the Discrete module of BayesTraits version 2 (Pagel and Meade 2006) via R v3.3.2 (R Core Team 2015) using the 'btw' package provided by Randi Griffin (2015).

As with many comparative analyses, it must be noted that this methodology detects correlation and correlation does not necessarily imply causation. It may of course be the case that two tightly correlated traits are not causally connected at all, or influenced by some third factor with little or no direct interaction. Nevertheless, where researchers have well-reasoned prior expectations that two traits have a causal relationship, strong correlations can be used as evidence in favour of this. The traditional statistical and logical rule that *correlation does not necessarily imply causation* holds that correlation is not *absolute proof* of a casual relationship but it can be considered evidence in favour of such a relationship.

Using a binary trait (advanced cognition in this study) as the dependent variable, traditional statistical analyses would use logistic regression to determine which independent variables predict whether a species exhibits advanced cognition or not. To control for the statistical non-independence of data points caused by shared evolutionary history, Ives and Garland (2010) developed phylogenetic logistic regression. Although powerful, the computational demands of Ives & Garland's (2010) method were large making analyses prohibitively slow for large

trees and datasets until the recent development of a linear time algorithm to run the regression models (Tung Ho and Ané 2014).

In Chapter three, I use the phylolm package (Tung Ho and Ané 2014) in R v3.3.2 (R Core Team 2015) to run a series of phylogenetically controlled logistic regressions to evaluate and compare the predictive power of different social, ecological and life history traits. Models are compared using the Akaike Information Criterion (AIC) scores which provide a measure of the information lost in the construction of a statistical model (Akaike 1973). Alone, AIC values carry no useful meaning but when compared, AIC provides a method for comparing models. The lower the AIC value, the less information is lost and therefore models with lower AICs more accurately describe the real-world process that generates the observed patterns of variation in the dependent variable. There is no universally accepted limit for what difference between AIC values is sufficient to determine which model is the better fit. However, the prevailing convention is that a difference of less than 2 implies no significant difference in the explanatory powers of the models.

2.4.2 Chapter Four: The social brain hypothesis and the thermogenesis hypothesis in Cetacea.

In Chapter four, I use the recently developed method of phylogenetically controlled path analysis to investigate the thermogenesis hypothesis and the social brain hypothesis for the evolution of large brains in cetaceans. In order to compare and evaluate these hypotheses, I use data on habitat temperature, species distribution, brain size, body size and social structure.

2.4.2.1 Data

To analyse the hypothesised correlation between sea surface temperature (SST) and brain size, Manger (2006) gathered SST data by overlaying cetacean distribution maps with maps of mean SST. These data were criticized for some inac-

curacies (Marino et al. 2008, Manger 2009). Here I use modern computational methods based on Geographic Information System (GIS) datasets to gather more accurate SST data. Geographic ranges of 87 cetacean species were downloaded from the spatial data webpage of the International Union for the Conservation of Nature (IUCN) (2016) as shapefiles (.shp). Data on SST were gathered from the most recent version of the World Ocean Atlas (Levitus et al. 2013) available from the website of the National Oceanic and Atmospheric Administration (NOAA). I downloaded the decadal average SST over 6 decades (1955-2012) at a grid resolution 0.25°. Each point in the SST data (plotted on a world map) is compared to the polygon(s) describing each cetacean's distribution. From the SST points that are overlapped by each species' geographical range, the minimum and maximum temperatures were recorded and used to calculate the range of temperatures potentially experienced by each species. This analysis was conducted using the packages 'sp' (Pebesma and Bivand 2005) and 'oce' (Kelley and Richards 2016) in R v3.3.2 (R Core Team 2015). Five species of river-dwelling dolphins (*Inia geoffrensis*, *Lipotes vexillifer*, *Sotalia fluviatilis*, *Platanista minor* and *Platanista gangetica*) could not be analysed using this method as the World Ocean Atlas does not cover the water temperatures of rivers. Data for *Platanista spp.* were gathered from Grzimek's Animal Life Encyclopedia (Hutchins 2003) and data for the remaining three species were taken from Manger's (2006) original analysis. All temperature data were log-transformed prior to analysis. When transforming the minimum habitat temperature data, we added 2 to each value to account for the presence of negative temperatures in the data which could be as low as -1.8.

Data on brain size and body size for 42 species of cetacean were taken from Montgomery *et al.* (2013) who compile data from across primary literature about cetaceans. Montgomery and colleagues (2013) gather data on both endocranial volume and brain mass, creating potential concerns about data quality since endocranial volume is an indirect measure of brain size and could introduce a source of error to the data. The nature of cetaceans can often make extensive,

well-sourced data difficult to come by as the group is difficult and expensive to study. Using species where endocranial volume data and brain mass were both available, Montgomery *et al.* (2013) showed that measures of endocranial volume showed no significant differences from measured brain mass, justifying the use of endocranial volumes to calculate brain mass using an assumed density of 1 g/cc^3. This is in keeping with other analyses in birds and mammals that show that endocranial volume is a very reliable proxy of brain volume (Iwaniuk and Nelson 2002, Finarelli and Flynn 2009, Gittleman 1986).

Studies that index social complexity simply as social group size can be criticized on the grounds that aggregations of individuals such as flocks of birds or herds of ungulates, which can be extremely large, may be incorrectly categorised as socially complex when in fact, compared to the number of individuals, little or no social interaction takes place within these aggregations (Acedo-Carmona and Gomila 2016). Furthermore, raw group size may be difficult to observe (as in many cetaceans) or fluid, resulting in potentially widely varying measurements that could cause contradictory results. Instead, social complexity may be more accurately indexed using descriptions of the types of groupings that species typically form. Where sufficient data are available, some researchers use a number of different measures of sociality to circumvent the problem including group size, mating system and social system (DeCasien et al. 2017). In Chapter four of this thesis, I adopt an approach to categorising cetacean sociality that combines social group size and group structure (May-Collado et al. 2007). Under May-Collado *et al*'s (2007) approach to cetacean sociality, species are assigned to one of four categories (described in table 2.1).

Table 2.1: Categorical classification of social structure taken from May-Collado et al (2007).

	Sociality	Defining Features of the Group
0	Solitary	Social bonds limited to mother and calf. Some aggregation for feeding, migration and breeding.
1	Group living	Weak/fluid associations. Both sexes disperse.
2	Group living	Long term associations with unrelated group members. Both sexes disperse.
3	Group living	Long term associations. Group members are close relatives. Sex-dependent natal philopatry or no dispersion.

In addition to the species categorised by May-Collado and colleagues (2007) under this system, I add classifications for six additional species based on the descriptions of their social organisations in volume 4 of the *Handbook of the Mammals of the World* (Wilson and Mittermeier 2014). Under this system of classifying species by social system, intermediate species with traits that appear to be drawn from two categories are categorised as intermediate (for example 1.5 is intermediate between state 1 and 2). All analyses using the social data are run with intermediate values rounded up and down to test for the sensitivity of the results to uncertainty in the data.

2.4.2.2 Phylogeny

The phylogeny of cetaceans has been the subject of extensive debate over a prolonged period of time. Morphological and genetic data have contradicted each other in the past, with early genetic studies placing mysticetes within odontocetes (Smith et al. 1996) rather than as sister taxa as suggested by morphology (Messenger and McGuire 1998, O'Leary and Gatesy 2008). Furthermore, the highly speciose group of species that make up the oceanic dolphins (Delphinidae) are thought to be the product of a rapid evolutionary radiation but the sequence and timing of many splits within this group were historically unknown (McGowen et al. 2009). A large, mammal wide supertree published in 2007 shows that many of the relationships within cetaceans are collapsed into large polytomies (Bininda-Emonds et al. 2007) demonstrating the uncertainty in cetacean phylogenetics. In particular, the oceanic dolphins and beaked whales are conspicuous, multi-species

polytomies as shown in figure 2.2 which is extracted from the 2007 mammal supertree (Bininda-Emonds et al. 2007). Supertrees are assembled from smaller phylogenies to create one, large phylogeny incorporating many groups(Sanderson et al. 1998).

The longstanding uncertainty around the evolutionary history of cetaceans was mostly resolved by a large analysis of cross-taxon data on 45 separate lines of molecular data including nuclear loci, mitochondrial genomes and transposon insertion events (McGowen et al. 2009). As figure 2.3 shows, this tree is well resolved and McGowen *et al.* (2009) found strong support for their topology.

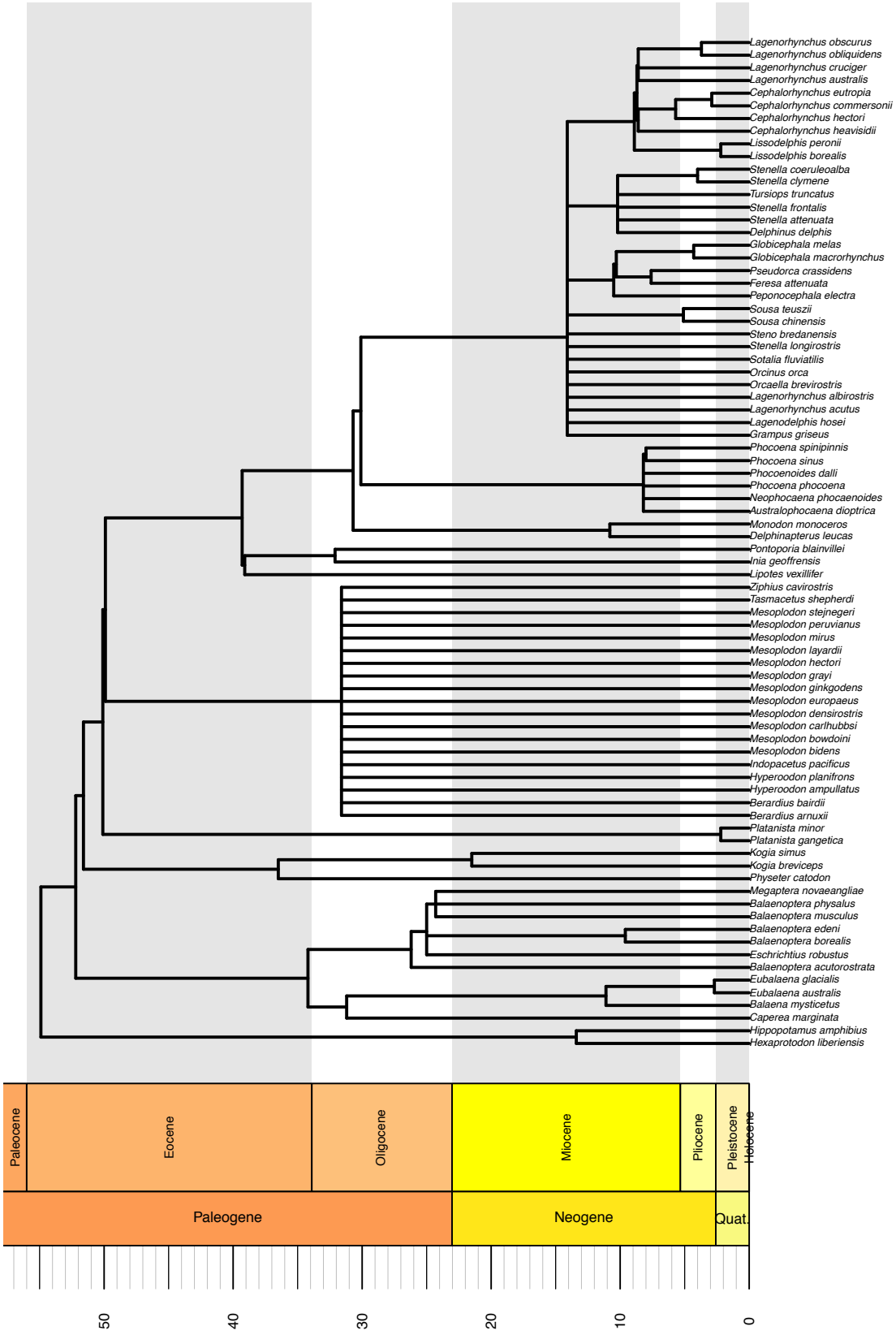

Figure 2.2: Phylogeny of cetaceans re-plotted from Bininda-Emonds et al. (2007) showing large, unresolved polytomies in the tree indicating uncertainty in the relationships of many cetacean species.

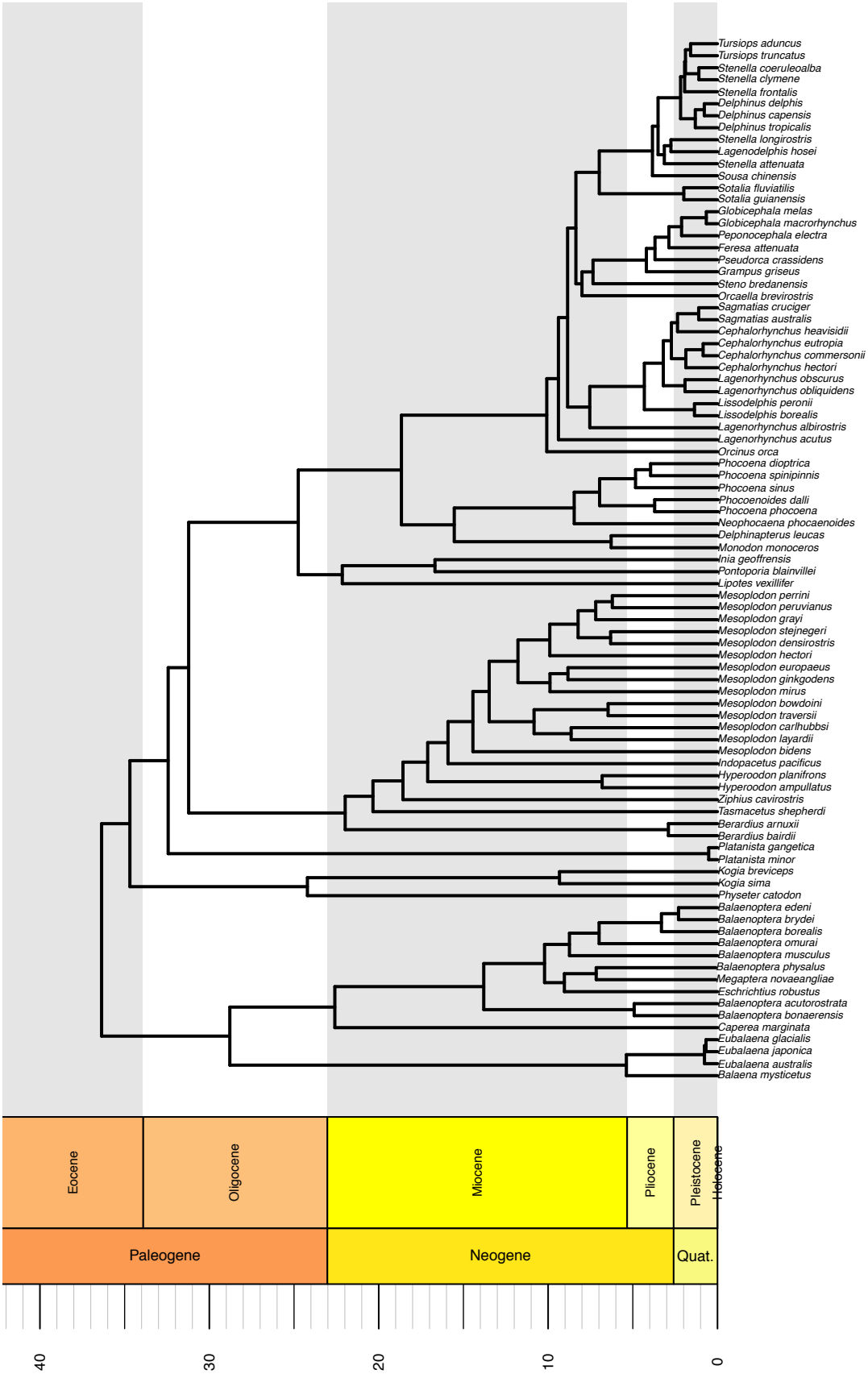

Figure 2.3: Updated phylogeny of cetaceans (McGowen et al 2009) showing a fully resolved and dated tree based on analyses of large amounts of molecular data.

2.4.2.3 Analysis

Traditional statistical analyses mostly evaluate the influence of one or more independent variables on a single dependent variable. In practice, the relationships between variables are complex and correlations between independent variables can violate the assumptions of the test being performed and cast doubt on the conclusions drawn. One method of analysis that deals with this problem is path analysis.

Path analysis is an extension of multiple regression in which regression models can be used to test complex interactions between numerous phenotypic traits (Shipley 2009). Path analysis begins with a directed acyclic graph (DAG) in which the variables of interest in the analysis are plotted on a flow chart with arrows connecting variables according to hypothesised and/or known causal relationships. An example of such a plot is depicted in Figure 2.4.

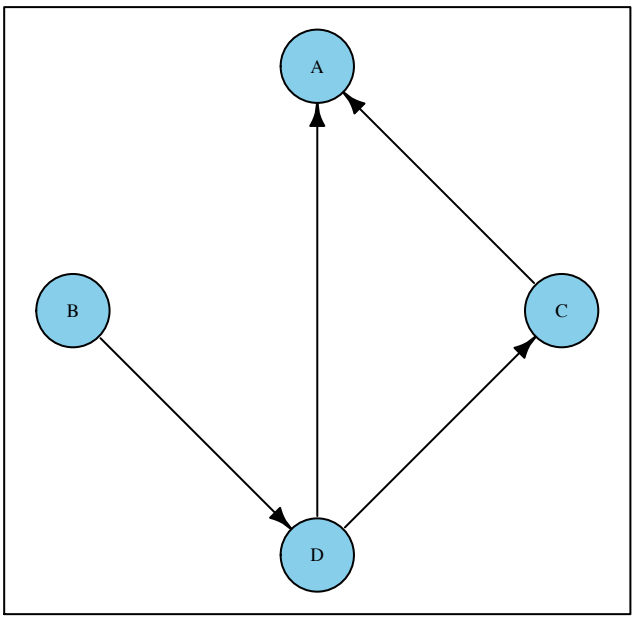

Figure 2.4: An example of a Directed Acyclic Graph (DAG) in which the hypothesised causal relationships between four variables are depicted. In this example, both variables D and C are hypothesised to influence variable A. Variable D also influences variable C and so a model describing the influence of D and C on A would suffer from correlation between explanatory variables.

The first step in the analysis is to identify variables that are not causally connected

and therefore, under the hypothesis described by the DAG, are causally independent according to the criterion of d-separation (Shipley 2000). In the example DAG, the variables A and B and the variables B and C are conditionally independent as they are not connected by arrows depicting causal relationships. The next step is to test whether these variables are truly independent using regression models. To construct these models, one of the pair is taken as the independent variable while the other is taken as the dependent variable along with any other variables that are causally linked to either one (Gonzalez-Voyer and Hardenberg 2014). In the example, one such model would take the form A = B + C + D.

If the hypothesised conditional independencies are correct and the two variables of interest are independent, variable B will not be a significant predictor of variable A. By combining the p-values testing each conditional independency and calculating Fisher's C statistic, the hypothesis depicted by the DAG can be either accepted or rejected as an appropriate hypothesis based on the result of Fisher's exact test (Gonzalez-Voyer and Hardenberg 2014).

The final step in the analysis is to construct models that describe the hypothesised causal relationships depicted in the DAG. Each variable in the DAG with an arrow leading to it from one or more other variables is the independent variable in one of these models and each variable that is hypothesised to have a causal relationship with the independent variable is included as a dependent variable. For instance, from the example DAG, these models would be as follows;

A = C + D

C = D

D = B

The combination of these models can then be compared using the C-statistic Information Criterion (CIC) (Gonzalez-Voyer and Hardenberg 2014) which is a statistic based on information theory and similar in concept to the widely utilised AIC (Akaike 1973). The lower the CICc value, the less information is lost by

the construction of the model and the more accurately the model describes the underlying processes producing the variation observed.

As with all comparative analyses, there is a need to control for the potentially confounding effect of phylogeny, which produces non-independence of data points because closely related species are more likely to resemble to each other than distantly related species. This is achieved by using Phylogenetic Generalised Least Squares (PGLS) regression (Grafen 1989) which corrects for phylogeny using a covariance matrix derived from the tree to determine how much of the relationship between traits is due to phylogenetic relatedness. All regression models in Chapter four are PGLS models performed in R v3.3.2 (R Core Team 2015) in the package 'caper' (Orme et al. 2013).

2.4.3 Chapter Five: Host-parasite coevolution and relative brain size in hosts of the cuckoo (*Cuculus canorus*) and cowbird (*Molothrus ater*).

In Chapter five, I test the largely unexplored hypothesis that host-parasite coevolution in birds has influenced the evolution of brain size by selecting for advanced cognitive abilities that aid potential hosts in avoiding or reducing the costs of parasitism. I gather data on the distributions of approximately 10,000 species of bird alongside diet and nesting behaviour in order to identify which species are at risk of being parasitised by two generalist brood parasites (European cuckoos and brown-headed cowbirds). I test the prediction that brain size evolution is influenced by the coevolutionary arms race using data on brain size, body size, vocal mimicry and migration.

2.4.3.1 Data

A large dataset of brain volumes and body sizes are gathered from the literature including primary measurements and compiled comparative datasets (Iwaniuk and Nelson 2003, Iwaniuk et al. 2004, 2005, 2010, Iwaniuk, Clayton, D., et al.

2006, Iwaniuk, Hurd, et al. 2006, Iwaniuk and Wylie 2006). The brain volumes in these data were measured as endocranial volumes. Iwaniuk and Nelson (2002) provide evidence that there is a strong positive correlations between endocranial volume and brain mass and, most importantly, that there is no significant difference in the results of analyses performed with either measure. This corresponds with similar arguments in mammals (Montgomery et al. 2013, Finarelli and Flynn 2009, Gittleman 1986) which show that cranial volume is a suitable proxy for brain size in mammals.

Each bird species is classified as social or solitary depending on the behavioural descriptions on the species pages of the online version of the *Handbook of the Birds of the World* (HBW Alive) (Del Hoyo et al. 2016). A species is defined as solitary if the animal is described as most often or always observed alone when foraging or roosting. Similarly, social species are those that forage and/or roost in groups. Vocal mimicry is defined here as the *ability to mimic the vocalisations of other individuals (either conspecifics or heterospecifics)* and data on the mimicry ability (1/0) of bird species are gathered from the vocalisations section of HBW Alive pages (Del Hoyo et al. 2016). Each species is classified as either *migratory* or *resident* in HBW (Del Hoyo et al. 2016) and these classifications are taken as the migratory status classification in Chapter five of this thesis.

Using the species' dietary descriptions in HBW Alive (Del Hoyo et al. 2016), each species is classified as either primarily *frugivorous* (fruit eating), *insectivorous* (insect and small arthropod eating), *nectarivorous* (nectar eating), *omnivorous* (generalist taking food from multiple categories), *granivorous* (seed eating), *herbivorous* (leaf/grass eating) or *carnivorous* (flesh eating). Similarly, the nest type of each species is classified as open, closed, cave or cavity based on the descriptions in the reproductive behaviour sections of HBW Alive (Del Hoyo et al. 2016). Finally, whether a species is parasitised by brood parasites or not is also taken from the reproductive behaviour section of HBW Alive (Del Hoyo et al. 2016).

In all cases where data is gathered from HBW, a classification is only made if the source text unambiguously describes the trait in question. In cases where a description is missing or based on too little information to make a clear statement about the trait in question, no data is recorded for that species.

Data on the geographical distribution and ranges of approximately 10,000 bird species were provided by BirdLife International (2014). The data were made available in the form of shapefiles (.shp), a data format for storing vectors that can be used to describe polygons which, when plotted onto a map, show the home range of a species. With these data, it is possible to overlay selected distribution maps and identify which polygons (and therefore in this case which species' ranges) overlap with each other.

First, the non-breeding range polygons of all migratory species (brood parasites and potential hosts alike) are removed from the spatial data since a species can only fall victim to a brood parasite where the breeding range of the species overlaps with the breeding range of the brood parasite. Next, the breeding range of the brood parasite is compared in sequence to every other species' breeding range in the dataset, searching for points within the polygons of each species that match with points within the polygon of the brood parasite. The output of this analysis is a list of species whose breeding ranges overlap with each brood parasite and therefore could be considered a potential host of the brood parasite. This analysis was performed using the package 'sp' (Pebesma and Bivand 2005) in R (R Core Team 2015) using the European cuckoo (*Cuculus canorus*) and the brown-headed cowbird (*Molothrus ater*) as the brood parasitic species.

It is clear that simply having a breeding range that overlaps with that of a brood parasite is a necessary precursor to being host to a brood parasite but is not sufficient to determine if a potential host is truly suitable. Therefore it is necessary to prune species from the list of potential hosts of those species which do not match the requirements of a brood parasite for a host. For this reason, I prune both the cuckoo and cowbird lists of potential hosts of any species that do

not match the diet of the brood parasite and do not have an open nest allowing for the laying of parasitic eggs.

2.4.3.2 Phylogeny

Historically, finding a well-resolved species level phylogeny of a group as large and diverse as birds, numbering approximately 10,000 species and occupying a huge diversity of environments across the planet, was extremely difficult. One way to address this problem is to stitch together a 'supertree' from smaller published phylogenies (Sanderson et al. 1998). This approach relies heavily on the availability of good trees from across the taxon, as was the case in mammals (Bininda-Emonds et al. 2007). However, in cases where a group is understudied or there is uncertainty about the phylogenetic relationships in the group, the supertree method can lead to unresolved, low information areas of the final tree (see subsection; Chapter Four: The social brain hypothesis and the thermogenesis hypothesis in Cetacea.).

In the case of birds, the group is thought to have radiated very rapidly early in the evolutionary history of the group (Ericson et al. 2006). Such periods of rapid diversification can lead to uncertainty in the relationships between species or higher groupings, as was historically the case in oceanic dolphins (McGowen et al. 2009). Because there is potentially a major source of uncertainty deep in the avian tree, detailed and taxonomically broad data is required to construct and accurate picture of the evolutionary history of the group. Jetz and colleagues (2012) used sequence data from 6,663 species, constraining the positions of the remaining 3,330 species based on known relationships, to produce a complete species level phylogeny covering all known bird species. The combination of extensive molecular data, knowledge gained from phylogenetic studies of higher taxonomic levels (Hackett et al. 2008) and powerful Bayesian analytic techniques allowed the creation of a large block of trees that provides a powerful tool for comparative analysis whilst not ignoring areas of uncertainty in the topology and

branch lengths of the tree (Jetz et al. 2012). For Chapter five of this thesis, I take a block of 1000 trees from the sample produced by Jetz *et al.* (2012).

2.4.3.3 Analysis

In Chapter five, I test a mixture of continuous and discrete variables to determine their relative influence on brain size in potential hosts of the brood parasitic cowbird (*Molothrus ater*) and cuckoo (*Cuculus canorus*). The most appropriate and commonly employed methodology to model the effects of multiple dependent variables on a continuous independent variable is Phylogenetic Generalised Least Squares (PGLS) regression (Grafen 1989). PGLS was originally developed as an extension of independent contrasts (Felsenstein 1985) and corrects for phylogenetic relatedness of data points in essentially the same way. Both approaches identify the degree of correlation expected from the structure of the phylogeny and weight the regression analysis accordingly using a covariance matrix.

In order to assess the potential effect of the branch lengths of the phylogeny on the analysis, I estimate the scaling parameter λ first. λ is a branch length transformation that serves as a measure of phylogenetic signal (Pagel 1999, Symonds and Blomberg 2014). A value for λ of 1, estimated by maximum likelihood using the package 'geiger' (Harmon et al. 2008) in R (R Core Team 2015), indicates that the branch lengths of the tree needs no transformation. Conversely, an estimated λ of 0 indicates no phylogenetic signal at all and the phylogeny would be transformed into a star phylogeny (all internal branch lengths would collapse to zero). Using the estimated value of λ to transform the tree appropriately, PGLS models are performed using 'caper' (Orme et al. 2013) in R (R Core Team 2015).

2.4.4 Chapter Six: Convergent evolution of large brains and advanced cognition: Identifying and quantifying the strength of convergence in Carnivora.

In Chapter six, I assemble a broad ranging comparative dataset on brain size, body size, life history, social behaviour and diet in terrestrial carnivores. I demonstrate the application of modern statistical methods to study convergent evolution of large brains within carnivora.

2.4.4.1 Data

Data on endocranial volume and body mass were compiled from literature sources (Finarelli and Flynn 2009, Isler and Schaik 2012, Lemaitre et al. 2009, Swanson et al. 2012, Damasceno et al. 2013). Endocranial volume is not a direct measure of brain size, which would require weighing freshly extracted or preserved entire brains (eg. Stephan et al. 1981). However, endocranial volume closely approximates brain volume in carnivores and mammals more generally (Montgomery et al. 2013, Finarelli and Flynn 2009, Jerison 1973, Gittleman 1986). The same is true of birds, where the use of endocranial volume rather than directly measured brain mass has no significant effect on the results of analyses (Iwaniuk and Nelson 2002). In carnivores, endocranial volume data seem to have broader taxonomic coverage than the sparse direct measurements of brain tissue and so for this study, endocranial volume is taken as a proxy for brain volume.

Group size data are collected from Gittleman's (1982, 1986) papers and supplemented with data taken from the species sociality descriptions in volume one of the Handbook of the Mammals of the World (Wilson and Mittermeier 2009). Gittleman (1986) defines group size as *the average number of individuals which regularly associate together and share a common home range.*

Additional quantitative data on carnivore diet and life history were gathered from PanTHERIA (Jones et al. 2009). Diet breadth is defined as the *number of dietary*

categories eaten by each species measured using any qualitative or quantitative dietary measure. Gestation period is defined as the *length of time of non-inactive fetal growth.* Interbirth interval is defined as *the length of time between successive births of the same female(s) after a successful or unspecified litter.* Litter size is defined simply as the *number of offspring born per litter per female.* Maximum longevity is taken as the *maximum adult age measured either through direct observation, capture-recapture estimates, projected from physical wear or unspecified.* The age at maturity is taken as the *age when individuals are first physically capable of reproducing* whilst the age at weaning is defined as the *age when primary nutritional dependency on the mother ends and independent foraging begins to make a major contribution to the offspring's energy requirements.*

2.4.4.2 Phylogeny

Although a complete, species level tree has been available for Carnivora for some time (Bininda-Emonds et al. 1999), the computational limitations of the time and the increase in availability of data since the first supertree was published mean that the original tree is out of date (Nyakatura and Bininda-Emonds 2012). Furthermore, since 1999 taxonomic understanding of carnivores has changed, splitting some species and lumping others. Also, the taxonomic coverage of available molecular data has expanded dramatically, necessitating an update to the phylogeny (Nyakatura and Bininda-Emonds 2012). The updated version of the tree presented by Nyakatura and Bininda-Emonds (2012) has fewer polytomies than the original tree and a well-supported topology. For the analyses presented in Chapter six, I use the updated species level supertree of Carnivora (Nyakatura and Bininda-Emonds 2012).

2.4.4.3 Methods

The study of convergent evolution, defined as the independent evolution of phenotypic similarity, is a broad ranging field with a great variety of methods. The first

step in any study of convergence is to identify which lineages actually represent examples of convergent evolution. In Chapter six, I use a broadly utilised model based approach for searching for convergence amongst quantitative data known as 'SURFACE' which stands for *SURFACE Uses Regime Fitting with Akaike Information Criterion to model Convergent Evolution* (Ingram and Mahler 2013).

The SURFACE method does not require the researchers to define particular niches in advance of the analysis. Rather, the input to the analysis is simply a phylogeny and phenotypic data. SURFACE begins at the root of tree, and fits Ornstein-Uhlenbeck (OU) stabilising selection models to the data (Hansen 1997, Ingram and Mahler 2013). This first phase is known as the *forward* phase of the analysis and starts with the entire clade experiencing a single selective regime. As the analysis proceeds forward in evolutionary time along the phylogeny and reaches branching points, new models are created inserting a new selective regime at the root of each new branch. The log-likelihoods of these new models are calculated and the models are compared to the previous model (without a regime shift) using the AICc score (which uses a correction for small sample sizes). The model with the lowest AICc score is selected, leading to the new regime being either accepted or rejected. This process is repeated until there is no further improvement of AICc and the best model is selected. This model will have a number of regime shifts (k) that denote shifts to new selective regimes across the phylogeny (Ingram and Mahler 2013).

Finally, the *backward* phase of the analysis proceeds from the tips of the tree to identify any selective regimes that are similar enough to be collapsed into the same regime. This is achieved by starting with the output of the forward phase and collapsing each pair of regimes in turn and recalculating AICc for each new model created by the collapsing of regimes. This procedure is repeated until further collapses would reduce the fit of the model rather than improve it. The output of this procedure will contain a number of distinct regimes (k'), which denotes the number of convergent regimes reached by multiple shifts, and the

number of shifts towards convergent regimes (c) (Ingram and Mahler 2013). The final product of SURFACE analysis is a tree with the regime shifts identified by SURFACE painted onto it, showing the distribution of convergent regimes and which lineages have converged. This approach will be used in Chapter six to identify convergent selection regimes in the evolution of brain and body size in carnivores.

Many methods utilised in the study of convergent evolution focus on identifying examples of convergent evolution and providing a sound statistical backing for claims of convergent evolution. Comparatively few methods quantify the strength of convergent evolution even though the strength of convergence is a fascinating topic for those interested in the adaptive consequences of convergence (Arbuckle et al. 2014, Stayton 2015a). The Wheatsheaf index (Arbuckle et al. 2014) measures the strength of convergence in one or more quantitative traits. The methodology requires that a *focal group* is defined. The focal group is the subsection of species in the analysis that occupy the same selective regime/ecological niche. The Wheatsheaf index takes the mean Euclidean distance between focal group species, plotted in phenotypic space, and compares this to the mean distance between any randomly selected species in the whole study group whilst controlling the analysis for phylogenetic relatedness using a covariance matrix (Arbuckle et al. 2014). If the focal group species are more similar to each other than to any random species, the Wheatsheaf index will be greater than 1 and this would be taken as evidence of strong convergence.

The Wheatsheaf index (W) is implemented in R (R Core Team 2015) using the 'windex' package (Arbuckle and Minter 2015). For the analysis presented in Chapter six of this thesis, I edited the code provided in the windex package to calculate the uncorrected Wheatsheaf index (W') as well. This is the same calculation as the original Wheatsheaf index but without phylogenetic correction (See Appendix for code). An uncorrected calculation of the Wheatsheaf index reveals the degree of similarity between the focal group and the group as a whole

without phylogeny, giving a measure of how similar the species that occupy a given niche are.

2.5 Summary

The methodologies and datasets described here are used throughout this thesis to conduct four studies into cognitive evolution across four different animal groups. All data collected is presented in its raw form in the appendix, except for the geographic data describing the species ranges of cetaceans and birds. These data are available on request from the websites of the IUCN (IUCN 2016) and BirdLife International (BirdLifeInternational and NatureServe 2014). Phylogenetic trees used in each analysis are plotted in full in the appendix.

3 Terrestrial living and the evolution of advanced cognition in Primates.

3.1 Abstract

The cause of advanced cognitive abilities of primates is often attributed to heightened sociality. The 'social brain' hypothesis proposes that ecological problems are solved by group living. Since additional problems are posed by living and competing within a group, sophisticated cognitive abilities are beneficial, driving brain expansion. Here I show that sociality is not the only causal factor in primate brain evolution. Using comparative methods, I investigated ecological, social and life history predictors of complex behaviours that are associated with high intelligence. The results presented here show that the evolution of enhanced cognition allowed some primate groups to adopt terrestrial lifestyles, suggesting that enhanced intellectual abilities preceded major ecological transitions in primate evolutionary history. Furthermore, the evolution of cognition is correlated with terrestrial living but not social living (rather than solitary living). Indicators of increased intelligence were found to be predicted by both social and ecological factors. These analyses indicate, in combination with other recent findings, that ecological and social variables are both associated with advanced cognition. I suggest that focusing on sociality as a complete explanation for primate cognitive abilities is inappropriate. Ecology and life history are also informative and add up to a more complex, inclusive view of primate cognition.

3.2 Introduction

Primates feature prominently in studies of animal intelligence, partly because many species exhibit apparently complex behaviours that are believed to reflect advanced cognitive abilities. Such behaviours include tool use (Ottoni and Izar 2008), tactical deception (Byrne and Corp 2004), innovation (Reader and Laland 2002) and even cultural transmission (Yamamoto et al. 2013) amongst others. In addition, primates tend to have large brains relative to their body size (Jerison 1973, Harvey and Krebs 1990, Barton and Harvey 2000) and the assumption is that energetically expensive brains (or brain parts) that are larger than expected for body size would have been favoured by natural selection on account of the adaptive advantages they confer (Striedter 2005). The logic that connects relative brain size, behavioural complexity and advanced cognition tends to take the following form: large brains promote cognitive abilities that, in turn, manifest in apparently complex behaviours.

Attempts to causally link brains to cognitive function have received criticism because such attempts commonly make the assumption that brain size (either whole brain size or the size of component parts) is a suitable metric of cognitive ability with little or no experimental validation of this assumption (Healy and Rowe 2007, 2013, Rowe and Healy 2014). However, several studies have since shown a relationship between complex behaviour and brain size, partly addressing the concerns over the sutability of brain size (Reader et al. 2011, Benson-Amram et al. 2016, Overington et al. 2011). A solution to this problem is to consider behavioural indicators of advanced cognitive abilities. The ability to respond to challenging or novel problems with flexible, innovative behaviour is indicative of the cognitive sophistication of an animal. Previous studies have used innovation (Reader and Laland 2001), tactical deception (Byrne and Corp 2004), tool use (Lefebvre et al. 2002), social learning and extractive foraging (Reader et al. 2011) as indicative of intelligence. Other potential indicators may include complex communication such as signature whistles observed in dolphins (Janik et al. 2006)

and cultural traditions (Herrmann et al. 2007). Cross-species comparisons of variation in, and the distribution of, complex behaviours have shown them to be statistically associated with the neural architecture that purportedly controls them (Güntürkün 2012, Lefebvre 2011), and a number of studies have found associations between brain size (or brain parts) and indices of behavioural complexity (Byrne and Corp 2004, Joffe and Dunbar 1997, Pawlowski et al. 1998, Kudo and Dunbar 2001, Reader and Laland 2002, Lefebvre et al. 2004, Lindenfors 2005), providing support for at least a partial relationship between brain size and cognition. In humans, data from magnetic resonance imaging (MRI) studies have revealed positive correlations between intelligence and brain volume (Luders et al. 2009), while Deaner et al (2007) found that measures of absolute brain size best predict cognitive ability in 24 non-human primate genera. Similarly, Benson-Amram et al (2016) reported that brain size predicts problem-solving ability in 19 species of captive mammalian carnivores.

A number of hypotheses have been proposed to explain the evolution of large brains and, by extension, advanced cognition in primates. The influential 'social intelligence' hypothesis (also referred to as the Machiavellian intelligence hypothesis) (Humphrey 1976) argues that the selective force that drove the evolution of large brains in primates was the adaptive challenge of anticipating, responding to and potentially manipulating the behaviour of conspecifics (Holekamp 2007, Byrne and Bates 2007). The related 'social brain' hypothesis (Dunbar 1998, 2009, Dunbar and Shultz 2007) argues that large brains (and complex cognition) are evolutionary consequences of sociality, which may have evolved as a response to predation or foraging selection pressures, which may have been solved by forming larger cooperative groups. A prediction of both the social brain and social intelligence hypotheses is that brain size should predict social group size (or other measures of social complexity). This prediction has been confirmed as larger brain size in primates predicts social group size (Dunbar 1992) as well as social complexity and network cohesion (Lehmann and Dunbar 2009). However, a recent study

using a large sample of primates found that diet, but not different measures of sociality, predicts brain size across primates (DeCasien et al. 2017), potentially casting doubt on the social brain hypothesis. The 'visual specialization' hypothesis (Barton 1996, 1998, 2004, 2007) proposes that variation in primate brain size is best explained by selection that acted on the visual system, notably during the transition from nocturnal to diurnal living. Barton (1998) found an association between encephalization and the parvocellular (but not magnocellular) system, which is associated with stereoscopic vision and detailed colour vision.

In contrast, ecological hypotheses (e.g. Harvey et al. 1980) assume that selection to survive in variable environments was the primary driver of cognitive abilities (i.e. large brain size) in primates. From this perspective, the demands of locating, monitoring and exploiting temporally and spatially distributed resources would have required complex cognition; so too the skills required to capture elusive prey and avoid predation (Lefebvre and Sol 2008). Evidence from beyond the primates has generally supported the idea of environmental determinants of brain size. In particular in birds, brain size has been shown to predict invasion success (Sol and Lefebvre 2000) and the environmental variability a species can tolerate (Sayol et al. 2016). These findings suggest that the complexties of certain ecological niches can directly drive brain evolution. These (and other) hypotheses that attempt to explain why primates have large brains (and the cognitive abilities that large brains permit) are often discussed as if they are mutually exclusive and/or contradictory. However, Dunbar and Shultz (2007) have pointed out that a number of potentially correlated factors could have combined in a non-additive way in the evolution of cognition. In their analysis, Dunbar and Shultz (2007) use a number of different variables potentially related to brain size in primates and performed a path analysis which showed that group size is best predicted by neocortex size, activity pattern and home range. This demonstrates the complexity of relationships between multiple variables and the difficulty of attributing the variation in a trait to a single causal relationship. Path analysis allows researchers to investi-

gate causal relationships amongst multiple interactions between those variables. For this reason, the method is a very powerful way of modelling complex interacting systems which are common in evolutionary biology. At present, a method for performing path analyses on comparative data is available for continuous data (Gonzalez-Voyer and Hardenberg 2014) but not for a mixture of discrete and continuous data. As this method is developed, it will become possible to address the evolution of sociality and brain size in the way Dunbar and Shultz (2007) suggest whilst correcting for the statistical nonindependence of data.

Furthermore, the hypotheses do not directly consider when complex cognition emerged, although Montgomery *et al.* (2010) partly addressed this latter issue in their ancestral state reconstructions of absolute brain mass, absolute body mass and relative brain size. They report strong evidence for increasing absolute and relative brain size – but not body mass – throughout primate evolution. In their reconstructions of proportional increases in relative brain mass they found that the terminal branches leading to the genera *Tarsius*, *Daubentonia* and *Galago* all had higher increases in relative brain size than the terminal branch leading to humans. The authors point out that this is notable as these three genera are no more socially complex than their close relatives, suggesting that sociality is not necessarily the sole factor in brain size evolution. Similarly, the reconstructions also revealed that at six points in the primate tree, the rate of increase of absolute or relative brain size is greater than the branch leading to humans. With the exception of one (located deep in primate evolutionary history along the branch leading to the ancestor of haplorhines), these high rates of change were reconstructed as predominantly having occurred during the Miocene epoch (Montgomery et al. 2010). During the Miocene epoch (approx. 23 – 5 mya) a trend of expansion of open grasslands and corresponding loss of forested areas continued (Retallack 2001). Climactic variation during this period and shifting habitat dynamics resulted in the extinction of many ape lineages in the late Miocene (Merceron et al. 2010). These considerable pressures and increasing

environmental variability have been argued to drive aspects of cognitive evolution in the human lineage during the late Miocene and on into the Pliocene and Pleistocene (Boyd and Richerson 2005).

Here I use phylogenetic comparative methods to investigate a combination of ecological, life history and social factors that have been implicated in the evolution of intelligence. I analyse possible causal relationships between them in an attempt to explain how and why advanced cognitive abilities evolved and place these evolutionary changes into context. I test a range of predictions derived from the four main hypotheses for the evolution of cognition in nonhuman primates.

3.3 Methods

3.3.1 Trait Data

Data on four behavioural traits (innovation, social learning, tool use and extractive foraging) were provided by Reader et al (2011) along with a measure of research effort (the number of studies published on each species in the Zoological Record database). These traits act as behavioural proxies for advanced cognition. These four behaviours were chosen above other behavioural traits because these data were gathered by a thorough search of primate behavioural literature encompassing a broad number of species with strict protocols governing the level of evidence required for a report of a given behaviour to be included (Reader et al. 2011). Each species in the data was then classified as either exhibiting advanced cognitive behaviours or not depending on the presence of one or more of these complex behaviours. Thus, for the purpose of this analysis, I define advanced cognition as the cognitive complexity required to perform at least one of these behaviours. Data of this nature are subject to bias created by different amounts of research effort being dedicated to different species. The standard method of correcting for this bias is to take the residuals from a log-log regression of the number of reports of the behaviour against the number of studies published on

the species (Reader and Laland 2002). This is not appropriate for a binary variable. In an attempt to correct the data for the potentially confounding effect of research effort, I eliminated all species with a research effort less than the lowest research effort among the species classified as exhibiting advanced cognition. This approach assumes that the lowest research effort amongst positively identified intelligent species is sufficient to determine whether a given species truly exhibits the behaviours in question.

A range of other variables were collected from the literature including social group size and social system (DeCasien et al. 2017), home range size (Jones et al. 2009, Nunn et al. 2004, Nunn and Barton 2000), maximum lifespan (Jones et al. 2009, Barton 1999, Lindenfors 2002), dietary breadth (Jones et al. 2009), activity pattern (Barton 1999, Kappeler and Heymann 1996, Nunn and Van Schaik 2002), habitat openness and terrestriality (Nunn and Van Schaik 2002). Dietary breadth is measured as the number of different food categories eaten by a species. Raw data are available in the appendix.

3.3.2 Phylogeny

I used the consensus primate phylogeny from version 3 of the 10ktrees project (Arnold et al. 2010). The tree is a well-resolved consensus tree from a Bayesian inference analysis of 17 genes. The version used in this analysis contains 193 species with branch lengths proportional to time.

3.3.3 Analysis

I used phylogenetic logistic regression to test four competing theories concerning the evolution of the primate brain (Ives and Garland 2010). With advanced cognition as the binary outcome, a model was built for each theory and run using the phylolm package in R (Tung Ho and Ané 2014). Models were compared using AIC scores. AIC was developed as a method of comparing different models

and provides a measure of information lost in a given model (Akaike 1973). AIC values are meaningless in isolation but can be compared to each other to determine which model best describes the process generating the variation in the outcome variable. Whilst there is no hard limit for a difference in AIC to be described as significant, the convention is that two models with a ΔAIC of less than 2 are not significantly different in terms of their explanatory power. Only species with data for all explanatory variables were used in this process, keeping sample size constant at 73 species for the purposes of model comparison.

To test hypotheses concerning the evolutionary scenarios that may have favoured enhanced cognition in primates, I used Pagel's method to construct two models of the evolution of two discrete characters using maximum likelihood: one model in which changes between the states of both characters occur independently of one another (4 parameter model) and one in which changes in each character are dependent on the state of the other character (8 parameter model) (Pagel 1994). Likelihoods of the independent and dependent models were compared to test for evidence of correlated evolution using a likelihood ratio test with degrees of freedom equal to the difference in number of parameters between models.

In order to test hypotheses concerning the causal relationships between traits, parameters describing specific transitions (the gain of general intelligence for example) were constrained to be equal regardless of the state of the second trait of the model. By comparing this model with the unconstrained dependent model, the influence of the second trait on transitions in the first trait was determined. This methodology allows us to test for the direction of causality and the temporal sequence in which traits were gained and lost (Pagel 1994). These analyses were performed using the Discrete module of BayesTraits v2 (Pagel and Meade 2006). For the purposes of this analysis, social system was dichotomised as solitary (0) and social (1) in order to study the origins of social living. It is important to note that this is not a test of the social brain hypothesis which explicitly predicts that increasing social complexity rather than the transition between solitary and

Table 3.1: Likelihoods of models of correlated evolution between advanced cognitive behaviour and four other traits alongside the results of a likelihood ratio test to compare the models. Significant results ($p < 0.05$) in the likelihood ratio test indicate that the dependent model is the better fit to the data, supporting correlated evolution between advanced cognition and the variable being tested.

Variable	Independent Model Log Likelihood	Dependent Model Log Likelihood	Likelihood Ratio	p-value
Sociality	-121.759	-118.955	5.607	0.231
Terrestriality	-157.203	-145.406	23.595	< 0.001
Habitat Openness	-121.938	-117.992	7.894	0.096
Activity Pattern	-133.198	-130.557	5.283	0.259

social living.

3.4 Results

Using Pagel's methodology (Pagel 1994) to test for variables that exhibit correlated evolution with intelligence, I found support for the coevolution of terrestrial living with advanced cognitive behaviour, but no association with social living, habitat openness or activity pattern (Table 3.1). Figure 3.1 shows the transition rates between the four possible states that the two characters, advanced cognition and terrestriality, can be in from a root state of no advanced cognition and arboreality. From this diagram it can be seen that this reconstruction best supports that transitions to terrestriality only happen in species that exhibit advanced cognitive abilities. Additionally, whilst there are frequent losses of advanced cognition in the tree as a whole, these occur at ten times the rate in arboreal than terrestrial lineages. The diagram shows changes in cognition occurring at relatively high rates in arboreal species but advanced cognition is never gained in terrestrial species (transition rate of 0). This demonstrates that although there are gains and losses of both traits throughout the tree, the probability of gains and losses in each state are dependent on the state of the other.

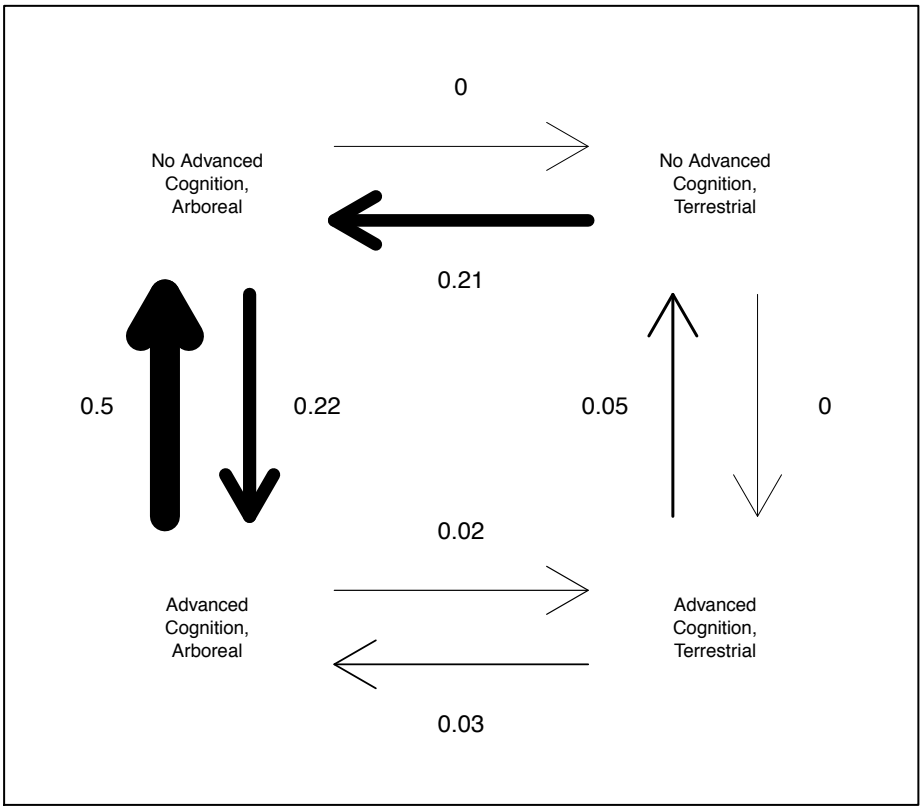

Figure 3.1: Path diagram showing transition rates between four possible states in which the binary traits advanced cognition and terrestriality can be. The transition rates demonstrate that transitions to terrestriality only occur from a state of advanced cognition.

Given that terrestrial living and cognition have been shown to be correlated, I conducted further analyses on the dependent model (in which transitions between states in one trait are dependent on the state of the second trait) in order to test causal hypotheses. I tested for directionality by restricting selected parameters to be equal and running a new model with one fewer parameter than the original dependent model. I was then able to compare the new model to the original (Pagel 1994). The results of these analyses are shown in table 3.2.

To test the proposal that transitions from arboreal to terrestrial living depend on the presence of advanced cognition, I restricted these transitions to be equal in species with and without advanced cognition and compared the new model to the original dependent model. A likelihood ratio test showed that the unconstrained model is the better fit to the data (LR = 4.849, p = 0.028), confirming that the presence or absence of advanced cognitive abilities do influence the probability

Table 3.2: Results of hypothesis tests to determine causal relationships between terrestriality and cognition. The constraints describe which transitions are constrained to be equal in order to test each hypothesis. The likelihood of each constrained model is the compared to the 8 parameter unconstrained model using a likelihood ratio test. A significant result in this test indicates that the constrained model is a worse fit to the data, provinding evidence in support of the hypothesis being tested.

Hypothesis	Constraint	Unconstrained Model Log Likelihood	Constrained Model Log Likelihoo	Likelihood Ratio	p-value
Transitions to terrestriality are dependent on the presence of advanced cognition	$q_{12} = q_{34}$	-145.406	-147.830	4.849	0.028
Transitions to arboreality are dependent on the presence of advanced cognition	$q_{21} = q_{43}$	-145.406	-146.939	3.066	0.080
Gains of advanced cognition are dependent on being arboreal or terrestrial	$q_{13} = q_{24}$	-145.406	-146.918	3.025	0.082
Losses of advanced cognition are dependent on being arboreal or terrestrial	$q_{31} = q_{42}$	-145.406	-147.945	5.079	0.024
Gains of advanced cognition precede transitions to terrestriality	$q_{12} = q_{13}$	-145.406	-153.895	16.979	< 0.001

of transitioning from arboreal to terrestrial. When I reversed the hypothetical causal relationship and constrained gains of advanced cognition to be equal, the unconstrained model was not a significantly better fit to the data than the new model (LR = 3.025, p = 0.082), indicating that gains of advanced cognition are not strongly dependent on being either arboreal or terrestrial. However, when I constrained losses of advanced cognition to be equal in arboreal and terrestrial lineages, this did significantly reduce the fit of the model (LR = 5.079, p = 0.024), confirming that losses of advanced cognition are much more likely to occur in arboreal lineages than terrestrial.

In order to assess the temporal sequence of the acquisition of advanced cognition and terrestriality, I constrained the gains of both to be equal. Comparing this with the unconstrained model it is clear that this constraint strongly reduces the fit of the model (LR = 16.979, p < 0.001). Therefore I conclude that transitions to

terrestriality were preceded by gains of advanced cognition in primate evolution. These results indicate that advanced cognitive abilities are a pre-requisite of transitioning to terrestrial living. Furthermore, since terrestrial species do not tend to lose their higher cognitive abilities as often as arboreal lineages in this model, I conclude that terrestrial living creates pressures that require high intelligence.

I ran phylogenetic logistic regression models to compare four alternative theories proposed to explain the evolution of advanced cognition. With advanced cognition as the outcome, four models were built based on the social brain hypothesis, the ecological intelligence hypothesis, the cognitive buffering hypothesis and visual specialisation hypothesis. The results of these models are presented in table 3.3. Significant relationships were identified for social group size, terrestrial living and lifespan. The only model that was not supported by this analysis was the visual specialisation model. These analyses suggest that a species is more likely to exhibit cognitively advanced behaviours if it lives terrestrially, in larger social groups and has a relatively long lifespan.

Table 3.3: Phylogenetic logistic regression model results including significance values for each predictor in the models and Aikaike Information Criterion values for each model. The difference between the AIC value for each model and that of the best-supported model (ΔAIC) is included for model comparison. An AIC > 2 indicates a significant difference between models.

Hypothesis	**Predictors**	**Coefficient**	**Standard Error**	**p-value**	**AIC**	**ΔAIC**
Social Intelligence	Intercept	-0.93	0.56	0.097	97.62	3.22
	Social Group Size	1.223	0.515	0.017		
Ecological Intelligence	Intercept	-1.31	0.954	0.169	95.93	1.63
	Dietary Breadth	0.223	0.201	0.267		
	Home Range	0.239	0.388	0.539		
	Terrestriality	1.787	0.847	0.035		
Ecological Intelligence	Intercept	-1.023	0.779	0.189	94.3	-
	Dietary Breadth	0.243	0.219	0.223		
	Terrestriality	2.087	0.772	0.007		
Visual Specialisation	Intercept	-0.768	0.734	0.296	100.51	6.21
	Activity Pattern	1.167	0.792	0.141		
Cognitive Buffering	Intercept	-4.757	2.069	0.022	96.74	2.44
	Lifespan	3.653	1.509	0.015		

By comparing AIC scores for these models, I conclude that the ecological models are marginally the best fit to the data. Two versions of the ecological models were

tested (with and without home range size) and the model without home range as a predictor was a slight improvement over the model including home range, but both had slightly better AIC scores than all other models. The ecological and social models differed in AIC by 1.62, implying no significant difference in the explanatory power of these models. It is worth noting that in the ecological models, only terrestriality is a significant predictor of advanced cognitive abilities. The lower AIC score of the most favoured model indicates that it has greater explanatory power (marginally) than the social model when predicting if an animal exhibits advanced cognition. The separation of these explanatory factors is arbritrary in a sense as it is perfectly reasonable to suppose that terrestriality, sociality and a number of other factors interact to influence cognitive evolution.

3.5 Discussion

Here I report two main findings: first, the analyses presented here reveal a strong association between the evolution of complex cognition and the transition to terrestrial living. Specifically, modelling of transition rates indicate that complex cognition in primates preceded the transition from arboreality to terrestriality. Reconstructions of the evolutionary history of primates yielded no evidence for correlated evolution of advanced cognition and the origins of sociality. Second, comparison of the phylogenetic logistic regression models suggest that a combination of ecological and social factors best explain the evolution of advanced cognition, which is consistent with Montgomery *et al*'s (2010) suggestion that social complexity alone is unlikely to have been the primary (sole) factor in primate brain evolution.

There are two possible evolutionary scenarios that could explain the finding that complex cognition preceded the arboreal-terrestrial transition. The first is that the transition from an arboreal to a terrestrial niche would have represented a significant ecological shift and only those species that already possessed advanced

cognitive abilities would have been capable of successfully making the transition. In this case, greater behavioural flexibility, which appears to be associated with complex cognition (Reader et al. 2011, Reader and Laland 2002), represents a preadaptation that may have allowed those species to successfully expand into the terrestrial niche. It is worth noting that the timing of the first major transition to a mainly terrestrial lifestyle coincides with ecological perturbation brought about by dramatic declines in temperature that characterised the end of the Miocene epoch (Retallack 2001, Merceron et al. 2010, Boyd and Richerson 2005). The maximum likelihood reconstruction of terrestriality (Figure 3.2) places two major transitions from arboreal to terrestrial living; one at the ancestor of cercopithecine monkeys and one at the ancestor of African great apes. These nodes are dated at 14.88 mya and 8.65 mya respectively in the 10ktrees phylogeny of primates (Arnold et al. 2010). Richerson and Boyd (2005) have argued that the increasingly variable environments that resulted from 'deterioration of climates' would have increased selection for traits that enhanced survivability, including complex cognition that would have underpinned the ability to adjust to novel conditions. They note that '*since the late Miocene epoch, organisms have had to cope with increasing variability in many environmental parameters at time scales on which strategies for phenotypic flexibility would have been highly adaptive*'.

The second scenario assumes that the initial transitions to terrestriality were not particularly cognitively demanding; that, at the time of the transitions, environmental pressures may have been sufficiently benign that the preadaptation (complex cognition) was neither necessary for, nor influenced, a species' ability to transition into the terrestrial niche. In this scenario, any post-transition ecological changes (e.g. shrinking forested areas associated with declining temperatures) would have introduced strong selective pressures on all fauna, but perhaps especially those species that had recently transitioned to a mainly terrestrial niche. The combination of a new and rapidly changing ecological niche would then have exerted strong adaptive challenges. Therefore, it is possible that those species that

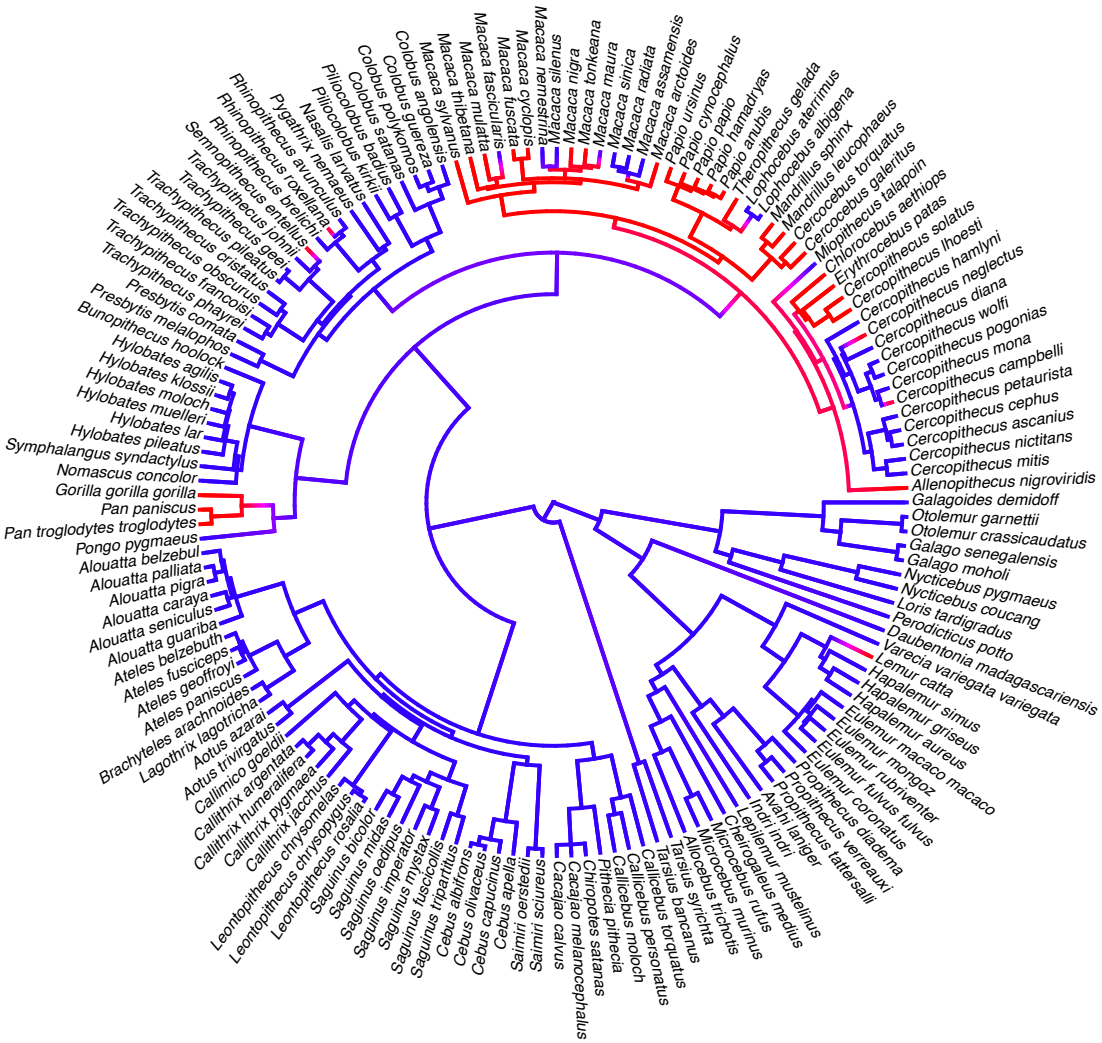

Figure 3.2: Density map showing the mapping of the binary trait terrestriality onto the primate phylogeny. The mapping is the product of 1000 stochastic mapping simulations combined and plotted onto the tree. Red denotes terrestriality whilst blue denotes arboreality.

did not possess complex cognition were unable to adapt to a rapidly changing terrestrial environment, leaving only those species that did possess the pre-adapted cognitive complexity. It is impossible to distinguish between these two scenarios based on the data presented here. In fact, when considering the comparative data, both scenarios would result in the same distributions of traits. The difference is the order of events in evolutionary history as to whether transitions to terrestriality were intitially benign and became more challenging after ecological changes or was always challenging. Given that terrestrial environments contain a variety of food resources, some of which require extractive foraging and, potentially, tool use to exploit (Visalberghi et al. 2005), greater behavioural flexibility would have been advantageous (and maintained by the multiple adaptive challenges of terrestrial environments). Whilst these traits are binary, being either present or absent, they are dependent on underlying cognitive complexity which evolves as a continuous trait (usually indexed by measures of brain size which are not included in this study). It is important to bear this in mind when considering these results. Here I am studying the evolution of a complex, continuously evolving trait by dichotomising it but this does not mean that gains of advanced cognition are an instantaneous jump from one state to another.

These findings do not challenge the existing consensus that primate brain size has been increasing over evolutionary time across the lineage, including changes much earlier in history than 15 and 9 million years ago (Montgomery et al. 2010). Nor do I claim that previous increases in brain size are unrelated to cognitive ability. On the contrary, the results strongly imply that cognitive ability (and by implication brain size) was undergoing evolutionary change across the primate tree before these major ecological transitions. What these analyses suggest is that the transition to predominantly terrestrial lifestyles (and other accompanying changes that would occur with such a niche shift) were either influenced or facilitated by the degree of advanced cognition exhibited by a given species of primate. When compared to other groups of mammals, primates are actually much

less terrestrial than ungulates and carnivores and yet have larger relative brain sizes and many more reported incidences of advanced cognitive behaviours. Therefore, it may appear that terrestriality by itself is not a particularly cognitively demanding lifestyle. Whilst terrestriality could provide cognitive challenges such as extractive foraging and even promote the evolution of more complex forms of tool use (Visalberghi et al. 2005), it is not simply spending more time on the ground that I hypothesise presented a selective pressure for primates. In fact, I propose that the challenges of shifting into a new niche, exacerbated by a changing climate, is what presented cognitive challenges to primates. The fact that other mammals did not necessarily respond in the same manner to such challenges could reflect that they may not have shifted niches in the same way. Alternatively, the different phenotypic starting points for other mammal groups during periods of changing ecological conditions could lead to different responses to selection pressures. Therefore, the apparent lack of correlation between terrestriality and brain size in other animal groups does not imply that terrestriality could not have influenced cognition in primates as the results suggest. Thus, it is not terrestrial living itself that appears to promote advanced cognition but rather the ecological pressures associated with such a shift. One such pressure could be an increased exposure to predators, which may in turn cause primates to live in larger groups, countering the threat of predation. If so, this would in fact support the social brain hypothesis which argues that primates solve ecological problems such as predation pressure by living in large groups which necessitates a larger brain (Dunbar 1998, Dunbar and Shultz {2017}).

The second main finding questions the long held view that sociality was the key factor in primate cognitive evolution. Although I did find a significant association between social group size and cognition (which is consistent with previous findings), I found no evidence of correlated evolution between advanced cognition and the origin of social living. Specifically, comparison of the regression models reveals that the two 'ecological' models both provide a similar fit to the

data as the social models. This finding is consistent with the social brain hypothesis which argues that complex cognition in primates was enabled by large brains that evolved in response to the problem of bonding large social groups (Dunbar 1998, 2009), which were made necessary by ecological pressures. In turn, behavioural flexibility and innovation could then have been deployed to solve other relevant ecological challenges. The analyses suggest a likely reversal of that causal sequence – that ecological factors drove the evolution of primate cognition which, in turn, may have been co-opted to bond large groups. As noted, the dichotomisation of sociality in this analysis is not an explicit test of the social brain hypothesis. In fact the classification of primate species as social or solitary may even appear misleading as even solitary primates do have some limited social relationships and so they could not truly be described as asocial.

The interpretation of separate regression models in this way is an imperfect approach to the study of evolutionary biology. Comparing four models as I have done here places each explanatory paradigm as separate explanations with equal biological status. In reality, this unlikely to be the case as the evolution of cognition (or any trait) is a complex system with many variables and relationships between them. It is possible that the multiple correlations identified in this analysis are not mutually exclusive and may reflect both causes and constraints on cognitive evolution. With this mind, a path analysis would seem to be a well suited method as employed previously to address similar questions around primate brain size evolution (Dunbar and Shultz 2007). Unfortunately, current methods for performing path analysis are yet to be fully developed for use with comparative data. A key feature of the analysis presented here is that I control for the statistical nonindependence of data points due to shared evolutionary history (See Chapter 2: Methods). The field of comparative methods moves quickly and a wealth of new methods have been developed to achieve this and thus reduce the type I error rate including a method for phylogentically controlled path analysis (Gonzalez-Voyer and Hardenberg 2014). This method is currently only suitable

for use on continuous data and cannot be used with a binary outcome variable as is used in this analysis. Future research will aim to perform such a path analysis in order to disentangle the complex web of relationships that surround primate cognition.

4 The social brain hypothesis and the thermogenesis hypothesis in Cetacea.

4.1 Abstract

Cetaceans (whales, dolphins and porpoises) have some of the largest relative brain sizes of any mammals. The social brain hypothesis posits that large relative brain sizes evolved in response to the challenges posed by living in increasingly complex social groupings. While the evolution of large brains in some cetaceans is attributed to the high degree of social complexity observed in these species, social living is not the only possible explanation. For example, the controversial "*thermogenesis hypothesis*" states that cetaceans' large brains are an adaptation to oceanic cooling at the Oligocene-Miocene transition 34.5 million years ago, providing heat through glial cell metabolism, and that they are not, in fact, cognitively complex animals. Here I use phylogenetic path analysis to directly test the social brain and thermogenesis hypotheses for the first time. Furthermore, I present the first comparative study of social structure and brain size in cetaceans. The analyses here show that, against expectations, both the thermogenesis hypothesis and the social brain hypothesis are supported by the available data. I explore the implications and alternate interpretations of the thermogenesis hypothesis in an attempt to account for the influence of habitat temperature on the evolution of large brains. I find a positive relationship between sociality and brain size seemingly weaker than similar relationships found in primates.

4.2 Introduction

Explaining the existence and distribution of energetically expensive, large brains in animal taxa remains an important issue in the study of cognitive evolution. A variety of hypotheses have been proposed and debated extensively. The social brain hypothesis holds that the cognitive challenges of social living drives the evolution of large brains (Dunbar 1998, 2009). In cetaceans, a competing, non-cognitive explanation for the evolution of large brains has been proposed known as the "*thermogenesis hypothesis*" (Manger 2006).

The social brain hypothesis holds that certain ecological problems (eg. predation pressure) can be solved socially and large brains and complex cognition have evolved to manage the resulting costs of social living (Dunbar 2009, Dunbar and Shultz {2017}). The strongest support for the social brain hypothesis comes from research on primates, in which species that live in large social groups have been shown to have larger neocortices relative to the rest of the brain (Dunbar 1992). Furthermore, neocortex size has also been shown to explain the relationship between male social rank and mating success in primates (Pawlowski et al. 1998), indicating that males with larger neocortices are more successful at navigating the social hierarchy and securing mating opportunities. There is taxonomically widespread support for a link between sociality and brain size (and by implication cognition). In fishes such as cichlids, social group size correlates with brain size (Pollen et al. 2007). The same relationship between group size and brain size appears in the Canidae (dog) family of carnivores (Finarelli and Flynn 2009). In addition, long-term monogamous pair-bonding in birds has been argued to drive the evolution of cognitive complexity (Emery et al. 2007).

In other taxa, the hypothesis has received mixed support. In birds, large relative brain size is associated with social monogamy (West 2014) pair bonding and bi-parental care (Shultz, S. and Dunbar 2010b). Amongst carnivores, the social brain hypothesis has been a point of contention, with some arguing for coevo-

lution between sociality and brain size (Perez-Barberia et al. 2007). However, reconstructions of carnivore evolutionary history show that the link between sociality and brain size is entirely driven by Canidae and in fact, more detailed analysis across the clade reveals no tight relationship between sociality and brain size (Finarelli and Flynn 2009). Analyses of chondrichthyan fish have shown that large relative brain size in batoids (rays and skates) and sharks is associated with habitat complexity (Yopak et al. 2007, Lisney et al. 2008), suggesting environmental determinants of brain size. Similarly in birds, brain size is associated with environmental variability (Sayol et al. 2016) and nest complexity (Hall et al. 2013), contradicting other researchers and challenging an exclusively social interpretation of brain size evolution.

In cetaceans, observations of complex sociality comparable to primates, such as male-male alliances in dolphins (Connor 2007, Connor and Krützen 2015) combined with observations of putatively cognitively complex behaviours such as tool use (Krutzen et al. 2014), may lead to the expectation that cetaceans fit a similar pattern to primates, in support of the social brain hypothesis. However, the social brain hypothesis has not been thoroughly investigated in cetaceans. No detailed comparative analysis of cetacean sociality has been performed, possibly because of the lack of sufficient data across the group, and so any claims of cetacean social intelligence rely on sparse evidence from a small number of species.

Manger (2006, 2013) argues that the vast majority of observations used to support claims of advanced cetacean intelligence are anecdotal and suffer from potential observer bias. In a lengthy review of cetacean behaviour, Manger (2013) argues that in fact, the behavioural repertoire of cetaceans is unimpressive with similar behavioural complexity found throughout the animal kingdom without accompanying claims of high cognitive ability. Therefore, the distribution of large relative brain size in cetaceans requires a non-cognitive explanation, which Manger provides through the hypothesis that cetaceans use their brains for thermal regulation and not advanced cognition. Manger (2006) argued that the cetacean

brain contains a high number of connective glial cells compared to computational neurons. Glial cells can assist in thermoregulation by increasing their metabolic rate in response to cold exposure (Szelenyi 1998). Manger therefore suggested that large brains in cetaceans evolved to deal with living in cold-water conditions. The thermogenesis hypothesis is consistent with the timing of the odontocete radiation which occurred at the Eocene-Oligocene transition approximately 34 million years ago, at a period of prolonged oceanic cooling (Zachos et al. 2001).

The thermogenesis hypothesis predicts that brain size should limit the temperatures a species can live in (hereafter referred to as habitat temperature) because species without relatively large brains would not be able to tolerate lower extremes of temperature. Manger (2006) provides support for this prediction, identifying negative associations between brain size and minimum habitat temperature and a strong positive relationship between encephalization and the range of habitat temperatures. These results showed that highly encephalized species live in a larger range of habitat temperatures, suggesting that expanded brain tissue is used as a flexible thermogenetic organ by species that experience large fluctuations in habitat temperature.

Manger's (2006) methods and conclusions have been criticised on a number of grounds. First, many cetacean researchers refute the dismissal of cetacean behavioural complexity (Marino, Lori et al. 2007b) and claim that the volume of observations in a variety of cognitive skills constitute sufficient evidence for advanced cognition. A review of the issue of dolphin cognitive abilities argued that although the purported examples of complex cognitive abilities in cetacea are often not unique to the group (similar and more impressive abilities being demonstrated in other mammals also), dolphins are "*in many respects cognitive generalists, performing at an overall high level.*" (Gunturkun 2014). The author goes on to suggest that high cognitive abilities have arisen independently in Odontoceti, Psittaciformes, Corvidae and Hominidae (Gunturkun 2014). Second, Manger's original analysis has been criticised for the lack of correction for

shared phylogeny (Maximino 2009). A reanalysis of a subset of cetacean data by Maximino (2009) appeared to refute any relationship between temperature and relative brain mass. However, the reanalysis was challenged since the dataset included two species incorrectly categorised as occupying temperatures below the freezing point of seawater (Manger 2009). The exclusion of mysticetes (baleen whales) and river dolphins from the analysis also limits its robustness by needlessly reducing sample size in an already data-poor taxonomic group. However, it should be noted that if the thermogenesis hypothesis is correct it should be detectable within the highly encephalized odontocetes given sufficient data. The thermogenesis debate has generated strong responses from both sides (Marino et al. 2008, Manger 2013) and remains an unresolved controversy that has implications for the evolution of cognition.

The representation of relative brain size in this debate has caused some confusion. Many studies of cetaceans, including Manger's (2006), have used encephalization quotient (EQ) which, in principle, gives a measure of brain size independent of body mass based on the scaling relationship between brain and body size (Jerison 1973). Using mammal-wide EQ values to study cetaceans can be dubious however, because cetaceans do not conform to the brain-body scaling law of all mammals (Manger 2006, Boddy et al. 2012). Other comparative studies of animal brain size have traditionally taken relative brain size (the residuals from a log-log regression of brain size against body size) as the method of controlling for body size. This method is in essence identical to calculating EQ and can be subject to the same criticisms. Furthermore, the use of relative brain size has been criticised because this involves using residuals as data which can result in biases in the outputs of statistical tests (Freckleton 2009). A more statistically appropriate approach is to include body mass as a predictor in any modelling rather than to try and control for its effects beforehand. In doing so, we are explicitly investigating the size of the brain relative to body size rather than simply the absolute size of the brain.

Contrary to a major pillar of the thermogenesis hypothesis, large relative brain size is commonly assumed to give rise to advanced cognitive abilities that manifest as complex behaviours. Interestingly, the assumption that enlarged brain size underpins increased cognitive abilities is not universally accepted (Manger 2013) despite the large number of comparative studies making this assumption (Healy and Rowe 2007). Brains are structurally complex and the assumption that wholesale increases in size result in commensurate increases in cognitive function has been criticised because of a lack of direct evidence linking brain size to cognition (Healy and Rowe 2007, 2013). In light of these criticisms, a large number of studies have investigated the distribution of apparently complex behaviours in a number of animal taxa and found strong associations between brain size and complex behaviours such as innovation and tool use in primates (Reader et al. 2011), problem solving in carnivores (Benson-Amram et al. 2016) and food caching in birds (Garamszegi and Eens 2004) amongst other behaviours (Byrne and Corp 2004, Lefebvre et al. 2002, 2004). The current consensus holds that large relative brain size is directly related to advanced cognition. However, it should be noted that none of these studies have focused on cetaceans and the cognitive complexity of cetacean behaviour is debated (Marino, Lori et al. 2007b, Manger 2013).

Perhaps surprisingly, the social and thermogenesis hypotheses have not been directly tested and compared in cetacea in a manner that allows us to evaluate the relative validity of either. Here I report a new analysis where I test the principal predictions of both the thermogenesis and the social brain hypothesis. I used phylogenetically corrected path analysis to evaluate three causal hypotheses concerning the relationships between brain size, habitat temperature and social group size. I used a species-level phylogeny of the cetacea to systematically control for the effect of phylogeny (McGowen et al. 2009). Addressing these questions using a modern statistical methodology gives insights into cetacean evolution and takes important steps towards resolving a hitherto unresolved debate in the study of brain size evolution.

4.3 Methods

4.3.1 Habitat temperature data

The original analysis proposing the thermogenesis hypothesis contained habitat temperature data for a limited number of species (Manger 2006). As discussed, the data used in this and subsequent analyses has been criticized both for innaccuracies (Manger 2009, Marino et al. 2008) and the failure to correct for statistical nonindependence of data points caused by phylogeny (Maximino 2009). The analysis presented here addresses both criticisms, first by re-gathering the habitat temperature data from an updated source and finally by using modern phylogentically informed statistical analysis. Here I follow a similar method to Manger's analysis and overlap ranges of each species with sea surface temperature data (Manger 2006). Data on sea surface temperature (SST) were taken from a more recent edition of the World Ocean Atlas (Levitus et al. 2013) available from the website of the National Oceanic and Atmospheric Administration (NOAA). I downloaded the decadal average SST taken over 6 decades (1955-2012) at a grid resolution of 0.25°. These data are plotted in Figure 4.1. Spatial distribution data in the form of shapefiles were downloaded for 87 species of cetacean from the IUCN spatial data webpage (IUCN 2016).

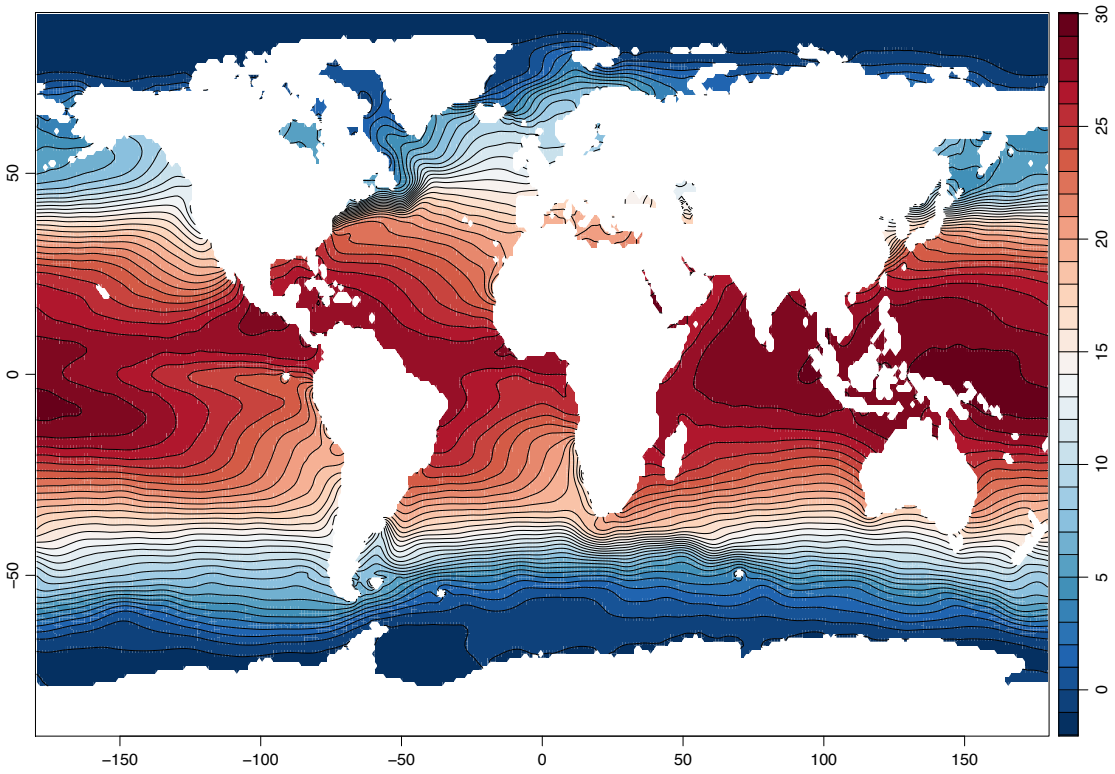

Figure 4.1: Plot of decadal average sea surface temperature derived from the World Ocean Atlas (Levitus et al. 2013). The geographic distribution of each cetacean species is compared against these data to determine the minimum and maximum habitat temperatures for each species.

Each point in the SST data was compared to the shapefile of each cetacean species to determine the minimum and maximum temperature potentially experienced by each species. The analysis was performed in R (R Core Team 2015) using the packages 'oce' (Kelley and Richards 2016) and 'sp' (Pebesma and Bivand 2005). The range of temperatures was calculated as the difference between the calculated maximum and minimum value for each species. Five species of river-dwelling dolphins (*Inia geoffrensis, Lipotes vexillifer, Sotalia fluviatilis, Platanista minor* and *Platanista gangetica*) could not be analysed using this method as the World Ocean Atlas does not cover the water temperatures of rivers. Data for *Platanista spp.* were taken from Grzimek's Animal Life Encyclopedia (Hutchins 2003) and the remaining three species from Manger's (2006) original analysis. All temperature data were log-transformed prior to analysis. When transforming the

minimum habitat temperature data, I added 2 to each value to account for the presence of negative temperatures in the data which could be as low as -1.8.

4.3.2 Social structure data

Here I adopt May-Collado *et al*'s (2007) "*broad concept approach*" to cetacean sociality in which species are assigned to one of four categories according to the size and structure of their social groups. I add to the earlier dataset by including information about six additional species (Wilson and Mittermeier 2014). May-Collado *et al*'s (2007) categorization of sociality (reproduced in table 4.1) describes an increasing scale of complexity in social structure. For the purposes of this analysis, I treat sociality as a pseudo-continuous variable including species classified as intermediate between two states as halfway between the two values. All analyses were performed with sociality rounded up and down to test the sensitivity of the analysis to uncertainty in the social structure data. These analyses are included in supplementary information. This method of classifying social complexity goes some way to addressing the justified concerns that raw group size is not necessarily a suitable index of complexity.

Table 4.1: Categorical classification of social structure taken from May-Collado et al (2007).

	Sociality	Defining Features of the Group
0	Solitary	Social bonds limited to mother and calf. Some aggregation for feeding, migration and breeding.
1	Group living	Weak/fluid associations. Both sexes disperse.
2	Group living	Long term associations with unrelated group members. Both sexes disperse.
3	Group living	Long term associations. Group members are close relatives. Sex-dependent natal philopatry or no dispersion.

4.3.3 Brain and body size data

Brain and body masses (in grams) for 43 species were taken from Montgomery *et al.* (2013) and log-transformed for analysis.

4.3.4 Phylogeny

In order to control for the potentially confounding effect of shared evolutionary history, I use a well resolved cetacean phylogeny from the literature including branch lengths proportional to time (McGowen et al. 2009).

4.3.5 Analysis

Path analysis is an extension of multiple regression developed to test interactions between multiple traits and make inferences about causality (Shipley 2009). Based on the thermogenesis hypothesis and the social brain hypothesis, I constructed two directed acyclic graphs (DAGs) to represent each causal hypothesis and a third to represent both hypotheses together. A fourth, null model was formulated in which the only variable that affects brain size is body mass. These causal models are depicted in Figure 4.2. In each model, body mass is linked to sociality. This link represents a correlation between body size and social group size in cetaceans. It is possible that such a correlation is driven by the different nutritional demands of groups. This relationship is not the subject of this analysis and so is present in every model.

Using the principle of d-separation (Shipley 2000), I identified pairs of variables that are not directly linked in each DAG and are therefore independent according to the model (Gonzalez-Voyer and Hardenberg 2014). These conditional independencies can be tested using regression models and subjecting the p-values of the coefficients describing the relationship between independent variables from each regression to Fisher's C test. If Fisher's C is not significant, then the model represented in the DAG can be accepted and the relative contributions of each variable can then be assessed using PGLS regression models (Gonzalez-Voyer and Hardenberg 2014). Models can be compared using CIC, an information theory approach to model comparison comparable to AIC. Here models are compared using CICc, which includes a correction for small sample sizes, using R code

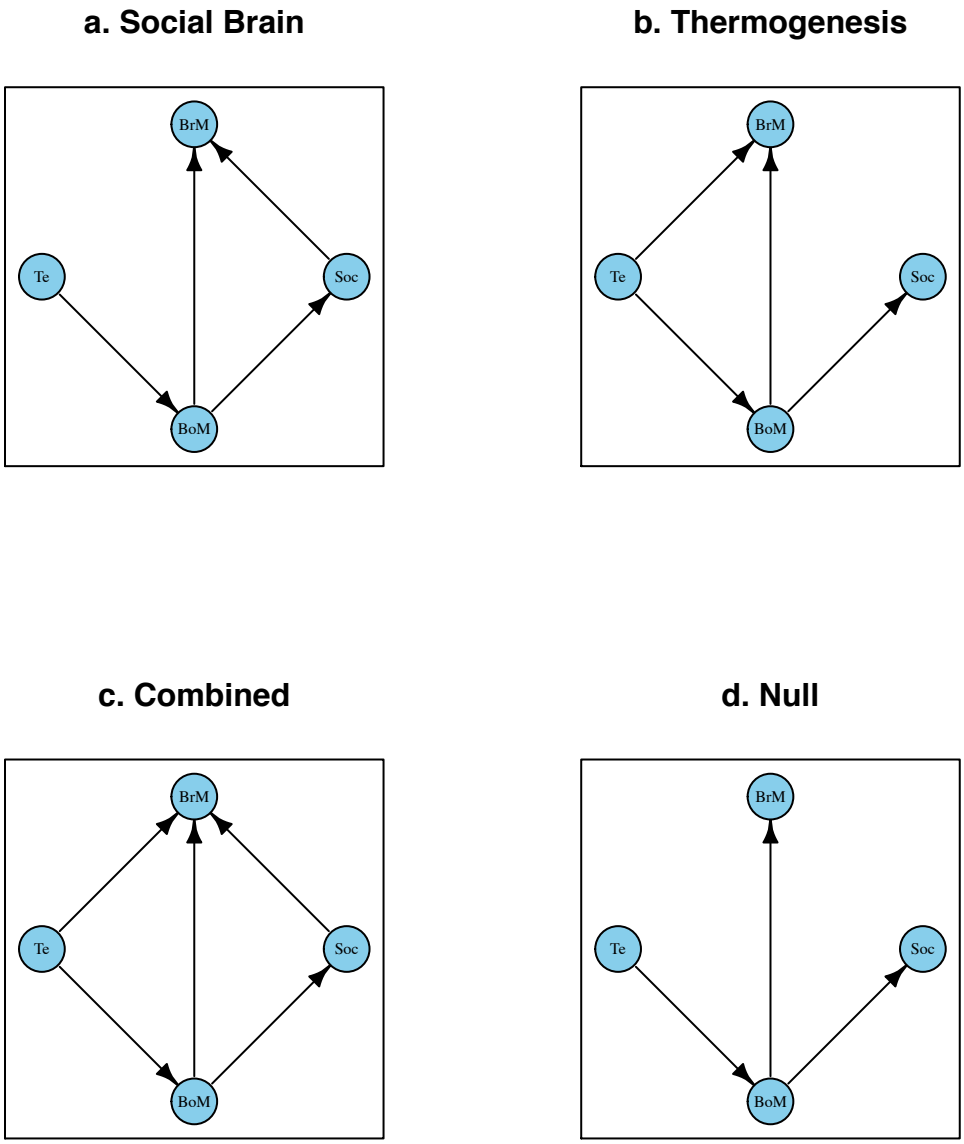

Figure 4.2: Four alternate models describing the hypothesised causal relationships between brain mass (BrM), body mass (BoM), sociality (Soc), and habitat temperature (Te) under the predictions of the social brain hypothesis (a), the thermogenesis hypothesis (b), a combination of the two previous hypotheses (c) and a null model (d).

provided by Gonzalez-Voyer and von Hardenberg (2014).

Analyses were run using minimum habitat temperature and range of habitat temperatures to test two alternative approaches to the thermogenesis hypothesis. The thermogenesis hypothesis predicts that large brains are a response to thermal pressures and so the thermogenesis hypothesis predicts that cetaceans living in lower minimum habitat temperatures will have larger relative brain sizes to act as a buffer against the extremes of temperature. Manger's (2006) original analysis found a stronger association between range of temperature and brain size than minimum temperature. A relationship between the range of habitat temperature and brain size could also be taken as supporting the thermogenesis hypothesis as the variable thermal pressures may drive the expansion of the brain as a flexible thermogenetic organ.

All regression models in this analysis were phylogenetically controlled PGLS models performed in R v 3.2.3 (R Core Team 2015) using the package 'caper' (Orme et al. 2013). The scaling parameter lambda was estimated using maximum likelihood in each model. When the data is pruned to exclude species with missing data, the sample size is 39 species of cetacean, including species from all families within cetacea.

4.4 Results

The principle claim of the thermogenesis hypothesis is that habitat temperature promoted the evolution of large brains for the purpose of generating additional heat when the animal is in particularly cold waters. Alternatively, the social brain hypothesis asserts that large brains evolved to increase the cognitive processing power required to live in larger, more complex social groups. Using the habitat temperatures experienced by cetacean species and a simple metric of social complexity derived from social structure, I tested these claims using phylogenetically controlled path analysis. The analysis was repeated using minimum habitat tem-

perature and range of habitat temperature habitats in order to thoroughly test the thermogenesis hypothesis (see Introduction).

4.4.1 Range of habitat temperature

A comparison of the social brain hypothesis, thermogenesis hypothesis, combined hypotheses and a null model is shown in table 4.2. The combination of the social and thermogenesis hypotheses emerged as the most favoured causal model. The null model was strongly rejected (C = 20.681, p < 0.001). Upon testing the conditional independencies of the thermogenesis model, sociality and brain size were revealed not to be independent (β = 0.08, p = 0.018) causing the model to be rejected (C = 11.383, p = 0.023). Similarly, when I tested the independencies of the social brain model, habitat temperature range and brain size were not independent (β = 0.27, p = 0.033), causing the social brain model to also be rejected. This analysis therefore rejects the possibility that either the social brain hypothesis or the thermogenesis hypothesis is exclusively correct.

Table 4.2: Results of phylogenetically controlled path analyses derived from four alternate path diagrams describing the social brain hypothesis, thermogenesis hypothesis, combined hypothesis and a null hypothesis using Fisher's C and CICc to order the hypotheses by degree of statistical support. These analyses use range of habitat temperatures as the measure of temperature

Model	C statistic	p-value	CICc
Combined	3.365	0.186	27.572
Social Brain	10.163	0.038	30.963
Thermogenesis	11.383	0.023	32.183
Null	20.681	0.000	38.294

For the combined hypotheses, I translated the path diagram into regression models describing the causal relationships. These models were tested by PGLS regression and the results are shown in table 4.3. The combined hypotheses model confirms that habitat temperature range does significantly influence brain size (β = 0.27, p = 0.03) as does social complexity (β = 0.08, p = 0.018). Figure 4.3 shows the combined model with the results added, clearly demonstrating the ef-

fect of both habitat temperature and sociality on the evolution of enlarged brain size. Despite the model comparison stage of the analysis (table 4.2) indicating that the social brain model is a slightly better fit than the thermogenesis hypothesis, the regression coefficients for each predictor indicate that temperature range ($\beta = 0.27$) has a stronger influence on brain size than sociality ($\beta = 0.08$). When rounding intermediate social complexity classifications up and down, I found that the values in table 4.2 changed marginally (See appendix) indicating that the results are not strongly vulnerable to uncertainty in the social complexity data.

Table 4.3: Results of PGLS models describing the hypothesised causal relationships between brain size, body size, sociality and habitat temperature range under a combination of the social brain hypothesis and the thermogenesis hypothesis.

Outcome	Predictor	β	Std. Error	p-value	λ
Brain Mass	Body Mass	0.384	0.038	0	0.87
	Temperature Range	0.268	0.121	0.033	
	Sociality	0.079	0.032	0.018	
Sociality	Body Mass	0.437	0.18	0.02	0.985
Body Mass	Temperature Range	0.764	0.502	0.136	0.964

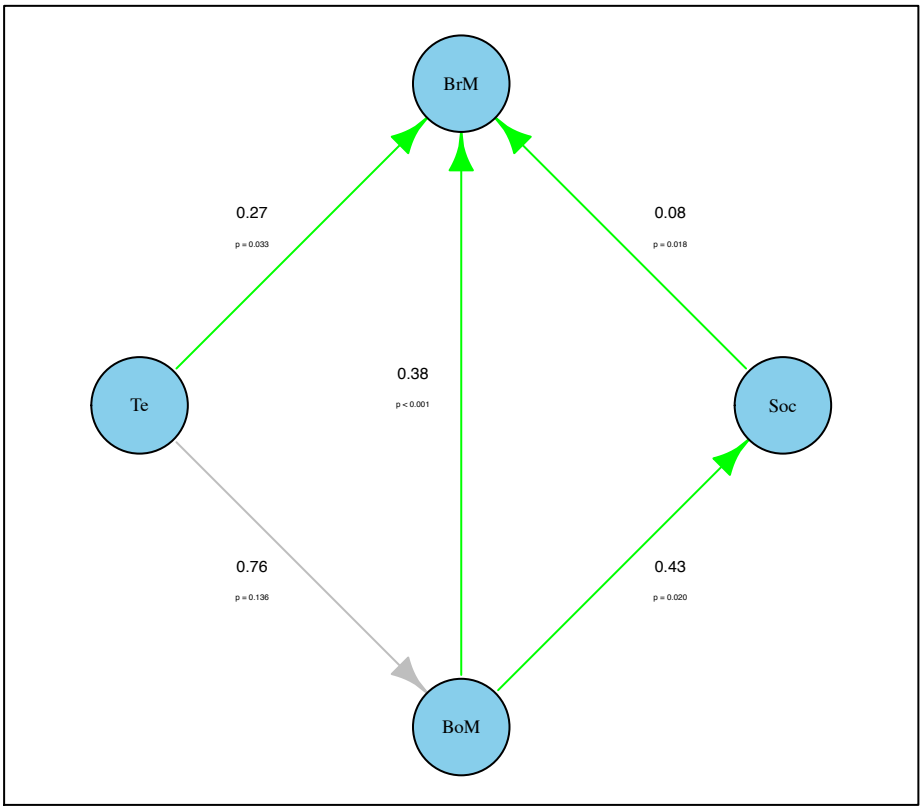

Figure 4.3: Path diagram with the results of PGLS regression models included showing the magnitude and significance of hypothesised causal relationships in a combination of the social brain hypothesis and the thermogenesis hypothesis. Statistically significant causal relationships are shown in green and non-significant relationships are depicted in grey.

4.4.2 Minimum habitat temperature

The results of model comparison when I used minimum habitat temperature are shown in table 4.4. As before, the null hypothesis is rejected (C = 14.11, p = 0.001) and the thermogenesis hypothesis is rejected (C = 10.811, p = 0.029). However, when minimum habitat temperature is used in place of the range of habitat temperatures, the social brain hypothesis is not rejected (C = 4.59, p = 0.332) and is slightly favoured over the combined model (C = 1.843, p = 0.398) with a difference in CICc of 0.66. Therefore, this analysis supports the social brain hypothesis slightly more than a combination of both hypotheses. However, adopting the convention from the use of AIC in model comparison, the ΔCICc of less than two indicates that one model cannot be favoured over the other based

on available evidence.

Table 4.4: Results of phylogenetically controlled path analysis of four alternate path diagrams describing the social brain hypothesis, thermogenesis hypothesis, combined hypothesis and a null hypothesis using Fisher's C and CICc to order the hypotheses by degree of statistical support. These analyses use minimum habitat temperature as the measure of temperature.

Model	C statistic	p-value	CICc
Social Brain	4.590	0.332	25.390
Combined	1.843	0.398	26.050
Thermogenesis	10.811	0.029	31.611
Null	14.110	0.001	31.723

Both the combined and social brain hypotheses were translated in to PGLS models once again. Table 4.5 shows the models describing the combined model with minimum habitat temperature representing the potential influence of habitat temperature on brain size. From these results, it is clear that sociality ($\beta = 0.09$, p = 0.01) has a significant influence on brain size but minimum habitat temperature does not (β = -0.05, p = 0.25). Table 4.6 shows the results of PGLS models describing the social brain hypothesis. The results of both analyses are visualised in figure 4.4, which demonstrates that minimum habitat temperature does not influence brain size, contrary to the predictions of the thermogenesis hypothesis, but does strongly influence body size (β = -0.54, p $<$ 0.001).

Table 4.5: Results of PGLS models describing the hypothesised causal relationships between brain size, body size, sociality and minimum habitat temperature under a combination of the social brain hypothesis and the thermogenesis hypothesis.

Outcome	Predictor	β	Std. Error	p-value	λ
Brain Mass	Body Mass	0.366	0.047	0	0.824
	Minimum Temperature	-0.052	0.045	0.253	
	Sociality	0.088	0.033	0.011	
Sociality	Body Mass	0.437	0.18	0.02	0.985
Body Mass	Minimum Temperature	-0.543	0.124	0	0.913

Table 4.6: Results of PGLS models describing the hypothesised causal relationships between brain size, body size, sociality and minimum habitat temperature under the social brain hypothesis.

Outcome	Predictor	β	Std. Error	p-value	λ
Brain Mass	Body Mass	0.399	0.039	0	0.86
	Sociality	0.091	0.033	0.01	
Sociality	Body Mass	0.437	0.18	0.02	0.985
Body Mass	Minimum Temperature	-0.543	0.124	0	0.913

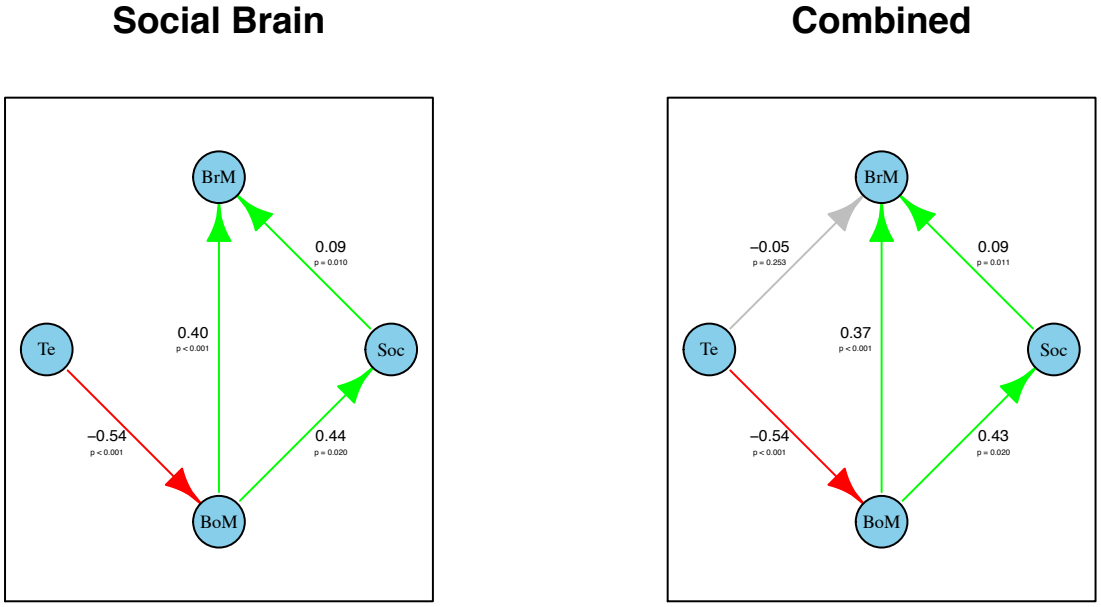

Figure 4.4: Path diagrams depicting the results of PGLS regression models showing the magnitude and significance of hypothesised causal relationships under the social brain hypothesis (left) and a combination of the social and thermogenesis hypothesis (right). Statistically significant positive causal relationships are shown in green, negative relationships in red and non-significant relationships are depicted in grey.

4.5 Discussion

I show by phylogenetically controlled path analysis that, against expectations, both social complexity and habitat temperature range positively influence brain size in cetaceans. However, minimum habitat temperature is shown to have no association with brain size. This analysis supports Manger's (2006) original analysis showing a correlation between habitat temperature range and brain size but contradicts the relationship found between minimum habitat temperature and

brain size in the same analysis. Furthermore, the relationship between social structure and relative brain size provides evidence in support of convergent evolution of brain size and, by inference, cognitive abilities in cetaceans and primates (Marino 2002).

4.5.1 The Social Brain Hypothesis

The social brain hypothesis is well documented in primates (Dunbar 2009) and has received mixed support from studies of other groups (West 2014, Perez-Barberia et al. 2007, Finarelli and Flynn 2009, Benson-Amram et al. 2016). Here I provide support for a link between the complexity of a species' social life and its brain size. The use of social complexity rather than raw group size is a more appropriate test of the social brain hypothesis because large aggregations of individuals may lead to a species being characterised as having a large social group despite the fact that little or no social interactions may take place (Acedo-Carmona and Gomila 2016). The measure of social complexity employed here combines social group size and social structure (May-Collado et al. 2007) in an attempt to circumvent the problems of using group size alone. The sample of 39 cetaceans was limited by the availability of detailed descriptions of social lives of cetaceans which may be difficult and expensive to gather for all species. As more detailed descriptions of cetacean sociality are published, it should be possible to characterise more aspects of cetacean societies and arrive at a more detailed metric of social complexity. Previous studies have found tentative links between odontocete EQ and social group size (Marino 1996) which can be argued to be qualitatively similar to relationships found in primates. The use of EQ to find the relationship between brain size and sociality cast considerable doubt on it as EQ derived from the mammalian brain-body allometric relationship (Jerison 1973) is an inappropriate measure of relative brain size since cetaceans do not conform to the general mammalian scaling law (Manger 2006). The analyses presented here do not rely on calculating EQ and as such more accurately represent brain size.

Contrary to the expectations of a strict interpretation of the social brain hypothesis, the effect size of sociality on brain size, whilst statistically significant, is small. Furthermore, when I adjusted the data to assess the potential effects of intermediate classifications of social complexity, both the effect size and statistical significance are slightly reduced when intermediate classifications are rounded down. Thus, although I offer support for a link between sociality and brain size, more detailed evaluations of cetacean social complexity are necessary in order to fully evaluate the social brain hypothesis in cetaceans. Further observations of wild cetaceans including orcas (Baird 2000), spotted dolphins (Elliser and Herzing 2014), sperm whales (Whitehead and Weilgart 2000) and humpback whales (Clapham 2000) have provided some detailed perspectives on the social lives of whales, revealing complex social interactions and behaviours. Observations of bottlenose dolphins have revealed complex, stable social structures (Connor et al. 2000) with persistent alliances (Connor 2007) and specialised roles within the group (Gazda et al. 2005). These features of dolphin sociality are argued to be similar in complexity to chimpanzee social behaviour (Connor 2007). Furthermore, descriptions of the odontocete neocortex seem to indicate that bottlenose dolphins (*Tursiops truncatus*), which are argued to be highly intelligent both in captivity and in the wild, have very high connectivity and plasticity in the neocortex as well as a relatively and absolutely large neocortical volume (Kern et al. 2011). The structure of the neocortex is of particular interest in the study of cognition as the neocortex is argued to be the seat of social cognition and executive function in primates (Shultz, S. and Dunbar 2010b).

A recent comparative study of the social repertoire of cetaceans has significantly added to the state of knowledge concerning this group. Fox *et al.* ({2017}) gathered data on cetacean brain size, social structure and cultural behaviours. Their analyses showed that encephalization in cetaceans is predicted by social structure and cultural repertoire, strongly supporting a social interpretation for cetacean brain evolution. This study supports the conclusions of Fox *et al.* ({2017}) and

adds to an emerging consensus that cetacean brain evolution parallels primate brain evolution in terms of a close connection to social complexity.

4.5.2 The Thermogenesis Hypothesis

The thermogenesis hypothesis was conceived as an explanation for the evolution of large brains in odontocete whales following a prolonged period of oceanic cooling (Manger 2006). Lower ocean temperatures were proposed to have favoured increased brain size for the additional metabolic heat generated, which would have acted as a buffer in a cooling ocean. The foundation of this hypothesis has been tested here and less definitively elsewhere (Maximino 2009, Marino et al. 2008) and has received mixed support. The analyses presented here supports a positive correlation between the range of habitat temperatures for cetaceans and their brain sizes and no correlation between minimum habitat temperature and brain size. This supports only one interpretation of the thermogenesis hypothesis, in which species that experience high variation in temperature across habitats evolve large brains as a flexible response to fluctuations in habitat temperature. In this interpretation, the large brain and high number of glial cells are used to generate heat whenever the animal experiences cold water temperatures. Such an explanation of large brain size evolution is unsatisfactory as the metabolic cost of a large brain is very high and must be borne constantly throughout an animal's life and not just when in certain environmental conditions, making this evolutionary scenario biologically unlikely.

The failure to find a link between minimum habitat temperature and brain size refutes the most common interpretation of the thermogenesis hypothesis which holds that cetaceans that live in lower extremes of temperatures need to generate additional metabolic heat and have evolved enlarged brains for this purpose. In fact, these results show that minimum temperature is strongly associated with body mass, supporting the assumption that the lower extremes of temperature contribute to the evolution of larger body size in cetaceans. This relationship may

be driven by the large-bodied mysticetes whose body size has been shown to have been evolving independently of brain size (Montgomery et al. 2013), a finding that is supported by the fact that minimum habitat temperature correlates with one but not the other. Furthermore, the evolution of gigantism in mysticetes has been shown to coincide with a prolonged period of glaciation which restricted habitats, potentially causing smaller bodied mysticetes to go extinct, leaving the large-bodied filter-feeding species as the only representatives of the group (Marx and Fordyce 2015). Thus it appears that the lower extremes of water temperatures have not influenced brain size evolution in cetacea. However, this does not necessarily refute the thermogenesis hypothesis entirely, as it may be the case that variation in habitat temperature is more important for the evolution of the brain as a source of metabolic heat.

A major assertion in support of the thermogenesis hypothesis is that cetaceans have a much higher glia-neuron index than other mammals (Manger 2006). This is taken as indicative of thermal pressures as glial cells can be used for thermogenesis in times of heat stress (Szelenyi 1998). Data on neuron number are limited and have been gathered using a variety of different methods which may not be reliably comparable (Marino et al. 2008). However, a simplified model of connectivity in the brain showed that increased glia-neuron indices arise naturally as the brain scales up under selection to increase in size (Jehee and Murre 2008). This model produced values close to empirical observations of mammalian brains (including cetaceans) and therefore seems to suggest that an increased glia-neuron index in cetaceans is not necessarily the product of direct selection on the number of glial cells used for thermogenesis. Rather, the proportion of glial cells would be expected to increase to maintain connectivity in an enlarged brain. Therefore, a higher glia-neuron index would be observed in larger brains regardless of whether the increased size implied increased cognitive complexity or increased heat generation capacity.

Manger also argued that cetacean brains do not exhibit the kind of structural

complexity of other large brained groups. Increasingly, the importance of broad taxonomic coverage in understanding the cetacean brain is being realised and a range of mysticete and odontocete brains have been studied in detail (Hof and Van Der Gucht 2007, Ridgway and Hanson 2014). These analyses have revealed some features of the cetacean brain that are unique to cetaceans such as a variant in the morphology of pyramidal neurons (tri-tufted variant) in the neocortex (Butti et al. 2015). The relationship of the particular morphology of these neurons to cognition is unclear. Across mammals, the complexity of pyramidal neurons is variable and clear correlations to cognitive abilities are not evident. A similar study on the giraffe (*Giraffa camelopardalis*) neocortex is argued to have revealed similar levels of cortical complexity to cetaceans and other mammals of equivalent body and brain size (Jacobs et al. 2015). Differences in structure and morphology are to be expected in groups as distantly related as primates and cetaceans which share a common ancestor 96 million years ago and such differences in morphology do not necessarily imply inferiority. The neocortex, which is argued to be the seat of social cognition, is expanded in cetaceans despite being significantly different in structure compared to primates, perhaps representing convergent evolution of advanced cognitive abilities in both groups (Marino 2002).

A key point of contention in this debate is whether cetaceans exhibit advanced cognitive abilities at all (Marino, Lori et al. 2007b, Manger 2013, Gunturkun 2014). It would seem that the finding that temperature range has a stronger influence on brain size than social complexity should cause us to lean towards the thermogenesis hypothesis and accept the claims of Manger (2013) that cetacean cognition is not particularly complex at all. However, I caution that the finding of a correlation between temperature range and brain size can equally be interpreted as evidence that variability in the environment has driven the evolution of advanced cognitive abilities as a buffer against a variety of environmental challenges. For example, a recent comparative analysis of over 1200 species of bird showed that large brains evolved when species invaded more seasonal, variable

habitats (Sayol et al. 2016). This logic could be applied to the results of this analysis to support the cognitive buffer hypothesis for cetacean brain evolution in which the dropping temperatures in Miocene-Oligocene oceans (Manger 2006) created a selection pressure on cetacea to which increased cognitive abilities were the evolutionary response. The mechanism of the cognitive buffering hypothesis, in which environmental challenges promote the evolution of advanced cognitive abilities as a buffer against those challenges (Sol 2009), differs markedly from the thermogenesis hypothesis in that it proposes that the brain expands to meet cognitive requirements rather than physiological. The range of habitat temperatures is just one aspect of environmental variability and, in isolation, is inadequate to formally test the cognitive buffer hypothesis. Future research should aim to distinguish between these alternative interpretations.

4.5.3 Conclusions

Debate over the thermogenesis hypothesis will continue to be beneficial, as it has provoked serious scrutiny of the cognitive credentials of cetaceans and the evolution of brain size in this famously encephalized group. Against expectations, I find evidence for a link between habitat temperature range and brain size, contradicting the findings of Maximino (2009) and Marino *et al* (2008) which claimed to refute Manger's (2006) findings. Therefore, I do not reject the thermogenesis hypothesis as others have but also, I do not necessarily support it as I have presented an alternative interpretation. The possibility that the correlation between habitat temperature and brain size is indicative of environmental variability, which can provide cognitive challenges (Sayol et al. 2016), provides a suggested direction for future research. The analyses presented here support a link between sociality and brain size in cetaceans which appears to be weaker than the comparable relationship found in primates (Dunbar 1992). These results justify the inclusion of cetaceans in discussions of social intelligence which was previously based upon detailed studies of very few species rather than compara-

tive evidence across the group. This debate will be further informed by detailed study of cetacean behaviour to determine their level of cognitive sophistication or lack thereof.

5 Host-parasite coevolution and relative brain size in hosts of the cuckoo (*Cuculus canorus*) and cowbird (*Molothrus ater*).

5.1 Abstract

Interspecific brood parasitic species avoid the costs of rearing young by having host species raise the young for them. Parasites and hosts are locked in an evolutionary arms race with each side adapting to overcome the other. Hosts are under strong selection to avoid being parasitised as the costs of rearing another individual's young are extremely high. Adaptations to avoid parasitism include the ability to assess the risk of parasitism based on environmental cues and the ability to discriminate parasitic eggs or chicks from those of the host. These abilities have an underlying cognitive component and therefore, it follows that host species cognitive abilities are under selection. Here I test the prediction that host species of two avian brood parasites (*Cuculus canorus* and *Molothrus ater*) will have larger brains than species with breeding ranges that also overlap that of the brood parasite and are therefore at risk of parasitism. Phylogenetically controlled analysis of brain size in potential host species shows that, against expectations, being parasitised does not appear to influence brain size evolution in birds. This mirrors the finding that brood parasitic birds tend to have smaller relative brain sizes than their close relatives. It is hypothesised that constraints on chick development in species locked in the parasite-host arms race restrict brain size evolution. The cognitive abilities involved in avoiding the risk of parasitism may be an example of cognitive complexity being decoupled from the expansion of brain tissue. Alternatively, it may be the case that the abilities exhibited by hosts are not especially cognitively complex.

5.2 Introduction

Brood parasites avoid the costs of rearing their young by passing them on to host species. Brood parasitism is a phylogenetically widespread reproductive strategy which occurs most famously in birds (Davies 2000) but also fishes (Baba et al. 1990, Sato 1986) and arthropods (Fucini et al. 2014, Cervo 2006, Boulton and Polis 2002). Brood parasitic species can be obligate brood parasites which can only rear young via a host, or facultative brood parasites which can rear their own young as well as parasitising hosts. Some (but not all) facultative brood parasites practice intraspecific brood parasitism, laying eggs in the nests of other members of their own species whilst obligate brood parasites must parasitise the nests of other species. Many interspecific brood parasites are specialists, such as indigobirds (*Vidua spp.*) parasitising a single host species. Some species, like the well-studied common cuckoo (*Cuculus canorus*) and cowbird (*Molothrus ater*) are generalist brood parasites, laying eggs in a number of different host species' nests.

In birds, intraspecific brood parasitism is more common than interspecific brood parasitism (Davies 2000, Yom-Tov 2001). Obligate interspecific brood parasitism has evolved independently seven times including once in Indicatoridae (17 species of honeyguide), once in Anatidae (black-headed duck), three times in Cuculidae (53 species of cuckoo) and twice in Passeriformes (19 species of indigobird, 1 species of cuckoo finch and 5 species of cowbird) (Sorenson and Payne 2002). In the most studied group, cuckoos, the evolution of brood parasitism has been shown to be the product of a shift to colonize seasonal, open habitats where the selection on reducing the cost of reproduction may be stronger than in ancestral tropical forested habitats (Krueger and Davies 2002).

Hosts of brood parasites incur heavy costs when parasitised. The strong fitness implications of being forced to rear another individual's young, either alongside or in place of one's own, have resulted in a variety of counter-adaptations to reduce

the costs of parasitism. The coevolutionary arms races between avian brood parasites and their hosts have been the subject of a great deal of research over a prolonged period of time. Coevolutionary arms races have been hypothesised to have dramatic influences on both host and parasite evolution.

Hosts can attempt to prevent a parasite laying by mobbing it (Feeney et al. 2012) and breeding in larger groups to increase nest defences (Canestrari et al. 2009). In fact, brood parasitism has been argued to be a contributing factor in the evolution of cooperative breeding (Feeney et al. 2013). Pre-laying or frontline adaptations to parasitism are predominantly concerned with recognising the danger of parasitism. The ability to recognise and respond to parasites has been shown to be socially transmitted (Feeney and Langmore 2013) and the risk of parasitism is determined by taking cues from the parasites themselves (Forsman and Martin 2009, Kleindorfer et al. 2013) or the environment (Welbergen and Davies 2012). Some hosts have alarm-calls specific to the parasite (Gill and Sealy 2004).

These strategies prompt responses from parasites. For instance, cuckoos reduce host mobbing behaviour by having barred patterning on their undersides that resemble a sparrowhawk (*Accipiter nisus*) (Welbergen and Davies 2011). Cuckoos have also evolved plumage polymorphisms to counter the social learning by the reed warbler (*Acrocephalus scirpaceus*) hosts of their mimicry (Thorogood and Davies 2013). In some cases, parasites are more direct and destructive, puncturing host eggs (Massoni and Reboreda 1999) and even withstanding the mobbing of the host until laying is completed (Gloag et al. 2013).

If the parasite is successful and lays an egg undetected, there are further adaptations at the egg stage of the arms race. Hosts are under strong selection to recognise their own eggs and reject foreign eggs (Langmore et al. 2005, Aviles and Garamszegi 2007). The identification and rejection of foreign eggs is achieved either by spotting the egg in the clutch that differs from the others, known as the discordancy hypothesis, or by comparing the eggs present in the nest to an

internal template of the eggs' appearance (Rothstein 1975). Hosts can distinguish parasitic eggs by colour (Aviles et al. 2010), size (Marchetti 2000), shape (Mason and Rothstein 1986), pattern (Stoddard and Stevens 2010, Stoddard et al. 2014) and even the position in the nest (Polacikova et al. 2013), although an experimental test found no evidence of egg arrangement predicting rejection (Hanley et al. 2015). These cognitive adaptations in the coevolutionary arms race between parasite and host have both been shown to contribute to egg recognition (Moskat et al. 2010), demonstrating that brood parasitism can strongly influence cognitive evolution.

In response to host adaptations, parasites have evolved thicker egg-shells to make them harder to puncture (Brooker and Brooker 1991) and sophisticated egg-mimicry to prevent hosts distinguishing between their own eggs and those of the parasite (Kilner 2006, Antonov et al. 2012). Egg mimicry appears to have driven the evolution of host races (known as gentes), where females specialize in parasitising a single host species, in the common cuckoo and the greater honeyguide (*Indicator indicator*). In honeyguides, host specialization appears to be a maternally inherited trait (Spottiswoode et al. 2011) and in cuckoos the races appear to be maintained by assortative mating (Gibbs et al. 2000). Other notable adaptations include that of the Australasian bronze-cuckoos which lay darkened eggs in enclosed, dome-shaped nests which hosts struggle to detect in the poorly lit nest (Langmore, Stevens, M., et al. 2009).

There is some evidence that retaliatory behaviour by parasites against species that reject their eggs helps slow the evolution of rejection behaviours, keeping the parasite ahead in the arms race (Soler et al. 1995, Hoover and Robinson 2007). This is known as "*the mafia hypothesis*" and is an example of a circumstance in which stronger defenses against parasitism can be costly, explaining why some hosts accept eggs from parasites. Parasitic eggs may also be accepted for other reasons. It is possible that the probability of making an error and rejecting a non-parasitic egg may be high, introducing a cost to rejection (Medina and Langmore

2016). Relatively new hosts of cowbirds tend to have little or no defenses against parasitism, even when heavily parasitised, seemingly showing that the new hosts have not had time to evolve defenses in an example of evolutionary lag (Hosoi and Rothstein 2000).

If a parasitic egg avoids rejection, some hosts can still reject the chick (Langmore, Cockburn, Andrew, et al. 2009, Sato et al. 2010), although many will fail to abandon the parasitised nest despite the fact that the parasitic chick may be much larger than the host. If a host uses imprinting to recognise its young, the costs of mis-imprinting would be so high that nestling recognition and parasite rejection could not evolve (Lotem 1993), potentially explaining why parasitic chicks are accepted. However, subsequent research showed that chick discrimination need not rely on imprinting as hosts can use cues such as the abnormally long fledging time of the parasitic chick (Grim 2007) and the perceived risk of parasitism (Langmore, Cockburn, Andrew, et al. 2009) thus allowing the host to abandon a parasitised nest.

In cases where the parasitic chick is accepted, a parasitic chick can eliminate the host chicks by evicting them from the nest or killing the brood directly (Spottiswoode and Koorevaar 2012). This approach allows the parasitic chick to monopolise the parental care of the host. Alternatively, parasites may co-exist with the host chicks. In cowbirds, the continued presence of host chicks is a benefit to the parasite as the large brood increases the provisioning rate of the host parent and, as it is larger than the foster-siblings, the cowbird is able to easily out-compete them (Kilner et al. 2004). In species where the parasite and host chick co-exist, the parasite may mimic the begging calls (De Marsico et al. 2012) or morphology (Langmore et al. 2011) of the host chicks. Although the traditional view is that parasite chicks mimic the hosts in order to reduce the chance of being rejected by the host parent, it has also been suggested that host chicks are mimicking the parasite in order to compete with it for food (Hauber and Kilner 2007). The presence of a parasitic chick may even be beneficial, leading to potential mutu-

alism between brood parasite and host. For example, the great-spotted cuckoo (*Clamator glandarius*) produces a secretion that repels predators (Canestrari et al. 2014).

Limited evidence has been uncovered describing the host-parasite arms race producing adaptations at the post-fledging stage of development. Fledgling screaming cowbirds (*Molothrus rufoaxillaris*) mimic the fledglings of their baywing hosts allowing the parasites to extract further parental care from the host (De Marsico et al. 2012).

Brood parasites choose hosts based on a broad variety of characteristics such as nest suitability (Soler et al. 1999), host suitability (Polacikova et al. 2009, Langmore and Kilner 2007, Grant and Sealy 2002) and host egg similarity (Cherry et al. 2007). Evaluating numerous aspects of the environment and potential hosts may seem like a cognitively complex task with many cues needing to be processed and compared in order to successfully parasitise a host and reproduce. However, studies of honeyguides (Corfield et al. 2013) and cuckoos (Boerner and Krueger 2008) have shown that brood parasites in both groups have smaller relative brain sizes than their close relatives.

One potential explanation for the smaller brains of parasites could be a trade-off with some other energetically expensive trait such as a longer gut to deal with a challenging diet (Corfield et al. 2013). Honeyguides are a monophyletic grouping of 17 species closely related to woodpeckers, all of which are brood parasitic and cerophagous (wax-eating). It may be the case that the beeswax diet of the honeyguides has driven them to have relatively small brains because digesting beeswax requires a longer digestive tract (Corfield et al. 2013). This explanation echoes the expensive tissue hypothesis that argues for a trade-off between brain size and gut size in primate evolution (Aiello and Wheeler 1995).

Similarly, it is possible that the reduced developmental period of parasitic chicks results in smaller relative brain sizes (Corfield et al. 2013). The life history of

a brood parasite dictates that chicks develop faster than other birds in order to allow the egg to hatch earlier than the host's eggs (Birkhead et al. 2011) and this may place strong constraints on brain development.

An alternate explanation for parasite brain evolution is that smaller relative brain sizes are linked to brood parasitism itself. Brood parasitic species do not engage in the cognitively and energetically expensive behaviours of constructing nests or provisioning their young. Evolutionary pathway analysis within the cuckoo family shows that brain size reduced prior to the evolution of brood parasitism, arguing against the idea that brain size may have decreased in response to brood parasites not having to provision their chicks (Boerner and Krueger 2008). This order of evolutionary events, with smaller brains preceding parasitism, may suggest that the relaxing of energetic constraints that accompany both parasitism and smaller relative brain sizes may have allowed cuckoos to exploit new niches (Boerner and Krueger 2008).

Potential host species that are able to recognise brood parasites and evaluate the risk of parasitism are more likely to be able to avoid or mitigate the costs of being parasitised. The extent to which a species can reduce the costs of parasitism is partly dependent on the cognitive abilities of the species, especially in the case of egg rejection. Rejecting a parasitic egg requires the ability to detect a parasitic egg, which may be mimicking host eggs or otherwise concealed. Attempting to identify the specific cognitive components of rejection behaviour has been an important area in the study of host cognitive abilities and their relationship to brood parasitism. Egg rejection is thought to involve learning as the time of a exposure to one's own eggs has been shown to influence rejection (Lotem et al. 1995). Similarly, reed warbler (*Acrocepahlus arundinaceus*) egg rejection ability improves at the second nesting attempt (Lotem et al. 1995), suggesting that long-term memory and learning contribute to a host ability to discriminate and reject parasite eggs.

The cognitive adaptations to brood parasitism lead to the prediction that expo-

sure to parasitism will select for enhanced cognitive abilities in hosts. An analysis of brain size in hosts of the common cuckoo experimentally added parasitic eggs to host nests to test the prediction that species with higher relative brain sizes (and by inference more advanced cognitive abilities) are better at identifying parasitic eggs and will reject the eggs at a greater rate (Aviles and Garamszegi 2007). The observation that smaller brained cuckoo hosts have higher rejection rates stands counter to the expectation that the host-parasite arms rate should select for advanced cognitive abilities in hosts. It may be the case that large brained species have escaped parasitism by virtue of their cognitive abilities (Aviles and Garamszegi 2007), in which case we would expect parasites to disproportionately exploit species with smaller brains. In this chapter, I present a different approach by comparing host species to non-hosts in order to test the broader evolutionary hypothesis that the coevolutionary arms-race between brood parasite and host affects brain size evolution.

Here I present analyses on species with breeding ranges that overlap with the range of the European cuckoo (*Cuculus canorus*) and brown-headed cowbird (*Molothrus ater*). I test two opposing predictions. The first is that species exposed to brood parasitism will evolve large brains to help reduce or avoid the costs of parasitism. The alternative prediction is that species who do not experience the pressures of brood parasitism will have larger brains, because brood parasites will have greater success parasitising small brained species with comparatively poor cognitive abilities.

5.3 Methods

5.3.1 Data

Data on brain volume (ml) and body size (g) were gathered from various primary sources (Iwaniuk and Nelson 2003, Iwaniuk et al. 2004, 2005, 2010, Iwaniuk, Clayton, D., et al. 2006, Iwaniuk, Hurd, et al. 2006, Iwaniuk and Wylie 2006).

Additional data on vocal mimicry (Present/Absent), sociality (Solitary/Social), migration (Migrant/Resident), diet and nest type were extracted from species descriptions from the online resource *Handbook of the Birds of the World Alive* (HBW) (Del Hoyo et al. 2016). Each species' diet was classified as primarily frugivorous, insectivorous, nectarivorous, omnivorous, granivorous, herbivorous or carnivorous based on the dietary descriptions provided in HBW. Similarly, each species nest type was classified as open, closed, cave or cavity nests. Sociality is included not as a test of the social brain hypothesis but rather of the prediction that living socially may be a response to the risk of parasitism mediated by the increased vigilance of a group.

Data on the ranges of more than 10,000 bird species were provided by BirdLife International (2014) in the form of shapefiles. The breeding range of each non-brood parasitic species was compared to the breeding range of the European cuckoo (*Cuculus canorus*) and the brown-headed cowbird (*Molothrus ater*) respectively to determine which species were potential hosts of the two parasites. This analysis was performed using the package 'sp' (Pebesma and Bivand 2005) in R (R Core Team 2015).

From the lists of species with overlapping breeding ranges with cuckoos, non-insectivorous species were removed as these species would not provide the correct diet for cuckoo nestlings and so are unsuitable hosts. Similarly, from the list of species overlapping with cowbirds, only species with primarily insect and seed-based diets were kept, matching the diet of the cowbird. From both lists of potential hosts, any species without an open nest structure was also removed as these species are unlikely to be suitable for parasitism.

5.3.2 Phylogeny

The phylogeny of birds has been an area of uncertainty due to the large number of species and extensive diversity within the group. Birds are thought to have

radiated very rapidly, early on in the history of the group (Ericson et al. 2006), making the relationships between clades uncertain. In the last decade, much progress has been made in constructing molecular phylogenies that begin to resolve the phylogeny of birds more clearly using data from representative species of each major bird family (Hackett et al. 2008, Prum et al. 2015). Here we use a species-level tree constructed by Jetz *et al* (2012) to control for the potentially confounding effect of phylogeny. In order to account for any uncertainty in the phylogenetic relationships between species, all analyses were run over a block of 1000 trees.

5.3.3 Analysis

The scaling parameter lambda was first estimated using the package geiger (Harmon et al. 2008) in R (R Core Team 2015) in order to assess the potential effect of different branch lengths in the phylogeny. Both for potential cuckoo hosts and potential cowbird hosts, lambda was estimated by maximum likelihood for each tree in the tree block. The maximum likelihood value was then compared to models in which lambda is fixed at 1 and 0, representing assumptions of Brownian motion and a star phylogeny respectively, using likelihood ratio tests. For both cuckoos ($\lambda = 0.986$, $p = 0.08$) and cowbirds ($\lambda = 0.998$, $p = 0.89$), the maximum likelihood estimate of lambda did not significantly differ from 1. Therefore in all subsequent analyses, λ was fixed at 1.

Body mass, sociality, vocal mimicry, migration and whether or not the species is parasitised were all entered as predictors of brain volume into phylogenetic generalised least squares (PGLS) models. PGLS models were run using the package caper (Orme et al. 2013) in R (R Core Team 2015).

5.4 Results

5.4.1 Potential Cuckoo Hosts

The mean results of the 1000 PGLS models for the European cuckoo hosts are shown in Table 5.1. The overall fit of the model is strong (F = 69.78, p < 0.0001). For potential hosts of the European cuckoo, only body mass (β = 0.61, p < 0.0001), vocal mimicry (β = 0.07, p = 0.047) and migratory behaviour (β = -0.12, p = 0.03) are significant predictors of brain size. In agreement with previous studies, migratory species are shown to have smaller brains (Sol et al. 2005, 2010). Furthermore species that exhibit vocal mimicry have slightly larger brains. Neither social vs solitary living (β = -0.002, p = 0.86) or being parasitised by the cuckoo (β = 0.1, p = 0.18) has a significant effect on brain size.

Since sociality was not informative in the maximal models, the PGLS models were rerun with sociality dropped. The results of these models are shown in table 5.2. The fit of the smaller models is stronger than the maximal models (F = 101.27, p < 0.001). As before, only body mass (β = 0.61, p < 0.0001), migration (β = -0.12, p = 0.02) and vocal mimicry (β = 0.07, p = 0.03) are statistically significant predictors of brain size. Being parasitised does not significantly predict brain size in the reduced models (β = 0.01, p = 0.16), yielding a similar effect size and significance as the maximal models.

Table 5.1: Mean results of 1000 PGLS models describing the predictive relationships of body mass, being parasitised by cuckoos, social vs solitary living, vocal mimicry and migration on brain size in potential hosts of the European cuckoo (*Cuculus canorus).*

Predictor	Beta	Standard Error	P-Value
Intercept	-0.9498	0.1075	0.0000
Body mass	0.6126	0.0315	0.0000
Parasitised	0.1050	0.0736	0.1636
Sociality	-0.0129	0.0402	0.7482
Vocal mimicry	0.0789	0.0361	0.0364
Migration	-0.1176	0.0552	0.0422
Body:Parasitised	-0.0644	0.0387	0.1066

Table 5.2: Mean results of 1000 PGLS models describing the predictive relationships of body mass, being parasitised by cuckoos, vocal mimicry and migration on brain size in potential hosts of the European cuckoo (*Cuculus canorus).*

Predictor	Beta	Standard Error	P-Value
Intercept	-0.9498	0.1075	0.0000
Body mass	0.6126	0.0315	0.0000
Parasitised	0.1050	0.0736	0.1636
Vocal mimicry	0.0739	0.0316	0.0258
Migration	-0.1222	0.0508	0.0219
Body:Parasitised	-0.0648	0.0377	0.0950

5.4.2 Potential Cowbird Hosts

The mean results of 1000 PGLS models for the cowbird hosts are summarised in Table 5.3. Like the cuckoo model, the overall model fit is strong ($F = 41.14$, $p < 0.0001$). In the cowbird models, only body mass is found to be a significant predictor of brain size ($\beta = 0.58$, $p < 0.0001$). Unlike potential cuckoo hosts, the potential hosts of cowbirds do not appear follow the pattern of migratory species having slightly smaller brains although the relationship is only narrowly non-significant ($\beta = -0.04$, $p = 0.09$). Both vocal mimicry ($\beta = 0.03$, $p = 0.51$) and sociality ($\beta = 0.01$, $p = 0.56$) do not significantly predict brain size. Being parasitised by a cowbird is a weaker predictor of brain size than in the cuckoo model ($\beta = -0.08$, $p = 0.46$)

Similar to the cuckoo host models, sociality is the least significant predictor in the models and so was dropped. The fit of these models is stronger than the maximal models ($F = 63.26$, $p < 0.0001$) and the outputs are summarised in table 5.4. Again, only body mass is a significant predictor of brain size ($\beta = 0.60$, $p < 0.0001$). As before, vocal mimicry is not informative in the model and so can be dropped for another set of models, shown in table 5.5. These smaller models were again a better fit than the larger models ($F = 84.94$, $p < 0.0001$). However, body mass is still the only significant brain size predictor ($\beta = 0.60$, $p < 0.0001$). Both migratory status ($\beta = -0.04$, $p = 0.09$) and being parasitised ($\beta = -0.06$, $p = 0.09$) are very weak, narrowly non-significant predictors of brain size. The trend in both cases is negative, suggesting resident species and non-parasitised

hosts have slightly larger brains but the lack of statistical significance means no conclusions can be drawn from these results.

Table 5.3: Mean results of 1000 PGLS models describing the predictive relationships of body mass, being parasitised by cowbirds, social vs solitary living, vocal mimicry and migration on brain size in potential hosts of the cowbird (*Molothrus ater).*

Predictor	Beta	Standard Error	P-Value
Intercept	-0.9976	0.1550	0.0000
Body mass	0.5874	0.0577	0.0000
Parasitised	-0.0833	0.1074	0.4550
Sociality	0.0123	0.0209	0.5603
Vocal mimicry	0.0327	0.0493	0.5109
Migration	-0.0361	0.0199	0.0898
Body:Parasitised	0.0145	0.0558	0.766

Table 5.4: Mean results of 1000 PGLS models describing the predictive relationships of body mass, being parasitised by cowbirds, vocal mimicry and migration on brain size in potential hosts of the cowbird (*Molothrus ater).*

Predictor	Beta	Standard Error	P-Value
Intercept	-1.0175	0.1251	0.0000
Body mass	0.5985	0.0420	0.0000
Parasitised	-0.0584	0.0350	0.1098
Vocal mimicry	0.0337	0.0485	0.4918
Migration	-0.0371	0.0195	0.0755

Table 5.5: Mean results of 1000 PGLS models describing the predictive relationships of body mass, being parasitised by cowbirds and migration on brain size in potential hosts of the cowbird (*Molothrus ater).*

Predictor	Beta	Standard Error	P-Value
Intercept	-1.0174	0.1246	0.0000
Body mass	0.5983	0.0418	0.0000
Parasitised	-0.0611	0.0346	0.0909
Migration	-0.0351	0.0192	0.0870

5.5 Discussion

The analyses presented here show that brain size in birds is not predicted by whether or not the species is parasitised by cuckoos (*Cuculus canorus*) or cowbirds (*Molothrus ater*). In potential host species of the cuckoo, resident species and those capable of vocal mimicry both had slightly larger brains than migratory species and non-mimicking species. The same weak trend was detected in cowbird

hosts for resident species (but not vocal mimics) but this trend did not reach the conventional threshold for statistical significance ($\alpha = 0.05$).

The hypothesis that parasitised species require advanced cognitive abilities to aid in avoiding the high costs of brood parasitism is not supported by this analysis. Previous research demonstrated that the level of parasitism in cuckoo hosts is not related to brain size, suggesting that the threat of brood parasitism in hosts does not create a selection pressure that acts on cognition (Aviles and Garamszegi 2007). Furthermore, Aviles and Garamszegi (2007) found that the ability to discriminate and reject parasitic eggs actually decreases as brain size increases in the hosts of the European cuckoo. A plausible explanation for these findings is that larger brained species evade parasitism through the evaluation of the risk of being parasitised and subsequent modification of behaviour. The analyses presented here show that there is no significant difference in relative brain size between hosts and non-hosts for either cuckoo or cowbird brood parasites, suggesting that brain size does not play an important role in determining which species are parasitised by cuckoos or cowbirds. This goes against the expectation that cognitive abilities (particularly innovation and behavioural flexibility) would aid potential hosts and allow them to escape brood parasitism.

In brood parasites themselves, it has been shown that cuckoos and honeyguides both have smaller relative brain sizes than their close relatives (Boerner and Krueger 2008, Corfield et al. 2013). In cuckoos, pathway models showed that reductions in brain size reduced the energetic demands of the birds, enabling a parasitic lifestyle (Boerner and Krueger 2008) whilst in the wax eating honeyguides, both diet and the reduced energetic requirements of having hosts raise the young have been suggested to contribute to the reduction in brain size compared to close relatives (Corfield et al. 2013). The results presented here demonstrate that despite the apparent cognitive demands of brood parasitism, brain size does not differ between hosts and non-hosts. Furthermore, the results add to previous studies on both sides of the arms race between hosts and parasites that show rel-

ative brain size does not conform to the expectation that increased cognitive load will necessarily promote the expansion of brain tissue over evolutionary time. It is possible that other features of brain anatomy, such as neuron structure or density, may provide a mechanism to allow for both reduced brain size and managing the cognitive complexities of the risks of brood parasitism. Alternatively, it is also possible that the cognitive challenges of brood parasitism have been overstated or can be managed by means other than advanced cognition and behavioural flexibility.

Both the common cuckoo and the brown-headed cowbird select their hosts non-randomly according to habitat features (Krueger 2007, Jensen and Cully 2005, Vogl et al. 2002, 2004). This suggests a strong selection pressure on potential hosts to avoid certain habitats or to increase anti-parasite defences around vulnerable habitats. Such a context-dependent response would seem to require a minimum level of behavioural flexibility and cognitive ability to evaluate and respond to the risk of being parasitised. As is shown here, this does not correspond with a difference in relative brain size, which has been shown to be a reliable predictor of innovation and cognitive ability across several animal groups (Overington et al. 2009, Reader et al. 2011, Benson-Amram et al. 2016). A possible explanation for this discrepancy is that exposure to brood parasites has put selection pressures on the host's development. In the arms race between parasite and host, the parasitic chicks of both cowbirds and cuckoos have evolved considerably shorter incubation times than hosts (Davies 2011, Krueger 2007, McMaster and Sealy 1998) potentially explaining the smaller relative brain sizes of brood parasites compared to their close relatives. Hosts of brood parasites may be under selection to reduce incubation time to counter the short development time of the parasitic chick, providing a similar explanation for the lack of increased brain size in host species locked in the arms race with brood parasites.

Migratory behaviour in both cowbird and cuckoo potential hosts shows a negative association with brain size, though only in the European cuckoo hosts does this

relationship reach significance. This finding is in agreement with previous research which showed that brain size has a negative association with migratory distance (Winkler et al. 2004, Sol et al. 2010). This relationship has been argued to be the result of energetic and developmental constraints on migratory species which must invest a great deal of energy into travelling long distances and often need to reproduce in short periods of time, reducing the developmental period available for brain growth (Sol et al. 2010). It is well established that both energetics (Aiello and Wheeler 1995, Isler and Schaik 2006) and developmental period (Iwaniuk and Nelson 2003) have played significant roles in the evolution of brain size. In addition to these factors, it can also be argued that small-brained species are driven to migrate because they lack the cognitive flexibility to respond to strong seasonal variations in the environment. Conversely, the pressures of a seasonally changing environment can be argued to have driven resident species to evolve larger brains for the purposes of behavioural flexibility. A recent large scale comparative study of birds demonstrated that across the group, species with large brains are more likely to live in highly variable environments, indicating that large brains are an adaptation to environmental variation (Sayol et al. 2016). A link between resident lifestyles and behavioural flexibility is supported by the finding that species which tend to exhibit behavioural innovations more frequently also tend to be resident rather than migratory (Sol et al. 2005). Disentangling the causes and consequences amongst these relationships is challenging.

Vocal mimicry is a complex behavioural trait that has previously been shown to be related to brain size in European passerines (Garamszegi et al. 2007). In agreement with these findings, this analysis shows that potential hosts of the European cuckoo that exhibit vocal mimicry have slightly larger brains than non-mimics. However, the potential cowbird hosts did not exhibit the same pattern, suggesting that the relationship between vocal mimicry and brain size in new world species may differ from European species. It may also be the case that the lack of a significant relationship is due to the comparative lack of vocal mimics

amongst potential cowbird hosts in the sample.

This analysis finds no relationship between predominantly social living (as opposed to solitary living) and brain size, seemingly contradicting the widely cited social brain hypothesis. This finding matches studies that show no relationship between group size and brain size in birds (Beauchamp and Fernandez-Juricic 2004). However, in birds it is not group size but the complexities of long-term pair-bonding that has been argued to relate to brain size and social bonding (Shultz, S. and Dunbar 2010a). The measure of sociality used in this analysis is a crude dichotomisation of a naturally complex phenomenon in two geographically defined subsets of birds and so this analysis does not truly test the social brain hypothesis at all. In fact, in this analysis the dichotomous variable describing sociality was intended to describe an anti-parasite defense (the increase in vigilance arising from group living). The analyses show that this is not a significant predictor of being a host to a brood parasite or not.

The fact that there is no significant difference in brain size between hosts and non-hosts could be interpreted in two ways. Either host cognitive complexity is not reflected in their brain size or hosts and non-hosts do not differ in cognitive complexity at all. Given the theorised influence on brain size evolution of the host-parasite arms race, it seems unlikely that host cognition is entirely uneffected by exposure to parasitism. It may be the case that developmental contraints have decoupled cognitive evolution from brain evolution, as argued here. It may also be the case that competing effects obscure the relationship between brain size and cognition in this case. If it is indeed the case that parasitised species are under selection to increase brain size and cognitive ability to mitigate the costs of parasitism, it follows that some species with large brains may have escaped parasitism in their recent evolutionary past, retaining their large brains and cognitive skills. This, combined with the fact that brood parasites would have greater success targeting species with smaller brains and poor discrimination abilities, leads to the suggestion that large brains may be a feature of species that have been exposed

to parasitism for a long time and species that have recently escaped parasitism. In this scenario, the current distribution of brood parasitic hosts, as analysed here, may not reveal a significant difference in brain size for two main reasons. The first is that large brained species may have recently escaped parasitism. The second is that brood parasites may target small brained species. In both cases, the differences in brain size between hosts and non-hosts would be obscured.

In conclusion, there is no evidence that the arms race between the brood parasitic cuckoo and cowbird and their various host species across their respective ranges has driven the evolution of large brains, and by implication advanced cognitive abilities, in hosts to avoid or reduce the extreme costs of parasitism. This echoes the findings on the other side of the arms race that brood parasitic birds tend to have smaller relative brain sizes than their close relatives. In the case of the parasites, the reduced development time of the chick necessary for brood parasitism is suggested to have placed constraints on the development of the brain. Similar constraints may be acting on the host chicks to restrict the amount of time available for brain development.

6 Convergent evolution of large brains and advanced cognition: Identifying and quantifying the strength of convergence in Carnivora.

6.1 Abstract

Convergent evolution, the independent evolution of similar phenotypes in two or more phylogenetically distinct taxa, is a widespread phenomenon and the subject of much study in evolutionary biology. The development of statistical methods to identify and quantify instances of convergence is fast-moving, with many innovative methods being published and debated. Large brains have evolved multiple times in many different lineages. The evolutionary roots of large brains have been the subject of extensive debate. The commonly cited social brain hypothesis states that the complexities of social living have driven the evolution of large brains and this hypothesis has received support from studies of primates, cetaceans and arguably other groups as well. However, studies from a broad variety of animal groups, including primates, have provided evidence in favour of alternate explanations for the evolution of large brains such as diet or ecological conditions. Here I gather data on the grouping behaviour, brain size and life history of terrestrial carnivores and analyse these data looking for patterns of convergence with modern phylogenetic methods. I show that in carnivores that occupy the same selective regime of brain and body size as the highly social Canidae, patterns of convergence do not conform to the predictions of the social brain hypothesis. Despite being similar in brain size and social group size, Canidae and Hyaenidae, two families of carnivore argued to contain examples of socially intelligent species, do not exhibit strong convergence in these traits when phylogenetic relationships are accounted for.

6.2 Introduction

Convergent evolution is defined as the independent evolution of phenotypic similarity. Convergence is an emergent property of a variety of evolutionary processes, although it should be noted that observing convergence does not necessarily imply an adaptive explanation (Speed and Arbuckle 2017, Mahler et al. 2017). Similarities in phenotype can be the result of chance, organisms experiencing similar environments and/or similar selection pressures, mimicry and a variety of other interspecific interactions (Mahler et al. 2017). The majority of studies into convergence are primarily concerned with questions over the evolutionary process that has resulted in convergent traits in extant species. However, convergence itself is not a process but a pattern, observable in the distribution of traits across the taxa of interest, meaning that the nature of any underlying evolutionary process can sometimes be debatable. An example of these issues can be seen in a recent review of evidence in favour of convergent evolution of advanced cognitive abilities in primates and carnivores (Holekamp and Benson-Amram 2017). Holekamp and Benson-Amram (2017) detail a number of similarities in brain size and social behaviour between cercopithecine monkeys and spotted hyaenas to present a strong argument not only that the similarities between the groups represent convergence, but that this case of convergence is the product of similar selection on social intelligence in both groups. It is worth noting that the authors do not claim that the same pressures act in the same way across animal taxa and thus argue that cercopithecine monkeys and spotted hyaenas represent an example of convergent evolution of the social brain (Holekamp and Benson-Amram 2017) as described by the social brain hypothesis (Dunbar 1998, 2009).

Large and complex brains have evolved independently many times in numerous animal lineages and the causes and consequences of the development of advanced cognitive abilities have been the subject of extensive research and debate (Roth 2015). The group most heavily scrutinised for their cognitive abilities is the primates. The cognitive abilites of non-human primates are prodigious. Primates

are known to use and make tools (Ottoni and Izar 2008, Visalberghi et al. 2009, Boesch and Boesch 1990, McGrew 2010), to understand intentional actions (Call et al. 2004, Phillips et al. 2009) and potentially possess some apsects of theory of mind (Povinelli et al. 1990, 1993). The ability to attribute mental states and beliefs to others, known as theory of mind, has been a topic of considerable debate with claims being advanced for primates (Tomasello et al. 2003, Povinelli and Vonk 2003) and birds (Bugnyar 2011). This apsect of cognition is thought to be particularly advanced as it relies on multiple complex cognitive skills. Amongst other mammals, cetaceans and elephants are also renowned for their large brains, although the extent of their cognitive abilities are less certain. Elephants have relative brain sizes and social complexity comparable to chimpanzees and some studies have shown that elephants are capable of innovation (Vidya 2014), social learning (Greco et al. 2013), self-recognition (Plotnik et al. 2010) and cooperation (Plotnik et al. 2011). However, elephants compare poorly to primates in tasks such as tool use and insight (Hart et al. 2008). Similarly, odontocete cetaceans such as killer whales (*Orcinus orca*) and bottlenose dolphins (*Tursiops truncatus*) have very large relative brain sizes and are capable of tool use (Smolker et al. 1997) and cultural transmission (Krutzen et al. 2014). However the range and depth of cognitive abilities of cetaceans have been debated with some claiming that dolphins have advanced cognitive abilites comparable to primates (Marino, Lori et al. 2007b, Marino et al. 2008) and others stating that their abilities have been overstated (Manger 2013).

Outside of mammals, there have also been independent evolutions of the pairing of large brains and cognitive abilities in birds. Most notably, the corvid family have displayed the ability to make and use tools and, as a result, have been compared to apes in terms of their cognitive complexity (Emery and Clayton 2004, Emery 2006). Remarkably, the New Caledonian crow (*Corvus moneduloides*) has been shown to exhibit metatool use, which involves using tools on other tools, an ability only previously observed in great apes (Taylor et al. 2007). Interestingly, raven

behaviour has been interpreted as showing attribution of mental states to others, a key aspect of theory of mind (Bugnyar 2011). In addition, rooks have been shown to solve problems by insight (Bird and Emery 2009). Psittacids (parrots) have also demonstrated advanced cognitive abilities including vocal learning (Pepperberg 2002) and tool use (Lambert et al. 2015).

The evolution of advanced cognitive abilities in primates, cetaceans and birds has been linked in each case to the evolution of complex sociality (*sensu* the social brain hypothesis). In primates, the neocortex ratio (the ratio of the size of the neocortex against the size of the rest of the brain) is positively correlated with social group size, strongly suggesting the need for advanced cognitive abilities in large social groups (Dunbar 1992). Many birds group in much larger numbers than primates, but forebrain size is not related to mean or maximum flock size, nor is it related with the propensity to form flocks at all (Beauchamp and Fernandez-Juricic 2004). However, it has been argued that the cognitive demands of extended social relationships between pairs, particularly the monogamous pair bonding species of birds, are the underlying social driver of the evolution of intelligence (Emery et al. 2007). In dolphins, long lasting male-male alliances comparable to those observed in chimpanzees have been advanced as evidence of social complexity which supports the contention of convergent evolution of social intelligence (Connor 2007).

There are other examples of large relative brain size in taxa that do not appear to conform to the predictions of the social brain hypothesis. For example, in marsupial mammals, large brain size has been shown to be the product of living in stable environmental conditions which permit greater energetic investment in brain development (Weisbecker et al. 2015). Curiously, there is no evidence that behavioural complexity plays any role in driving the evolution of large brains in marsupials raising the question of why an animal would grow a large, costly brain without evolutionary pressure to do so. Weisbecker *et al.* (2015) propose that the cognitive buffering hypothesis may solve this problem. The cognitive

buffering hypothesis holds that growing a large brain has survival advantages as it confers a degree of behavioural flexibility that can be deployed to solve environmental challenges (Sol 2009). Thus, marsupials are argued to have evolved large brains directly for the general survival advantages they confer rather than to solve some specific problem as in the social brain hypothesis. In birds, it has been recently argued that rather than social bonding, environmental variability has driven the evolution of large brains (Sayol et al. 2016). This suggests that environmental challenges can directly drive the evolution of large relative brain size in birds rather than influencing the bird's brains indirectly by driving the evolution of sociality as proposed by the social brain hypothesis (Dunbar 1998). Insects with enlarged mushroom bodies, such as hymenopterans (bees, ants and wasps), exhibit excellent spatial orientation and learning (Pahl et al. 2010). Although this was once considered a product of the advanced sociality of certain hymenopteran species, subsequent analysis revealed that in fact, spatial learning and navigation were ancestrally under strong selection in this group of insects for the purposes of parasitoidism (Farris and Schulmeister 2011). The famously large brained cephalopods (octopuses and squids) have evolved advanced cognitive abilities such as spatial memory, learning (Hochner et al. 2006) and tool use (Finn et al. 2009). Although capable of social learning (Fiorito and Scotto 1992), there is no suggestion that cephalopod brain size is related to social complexity but rather, it is more likely that cephalopod cognitive abilities are the product of their predatory lifestyles (Roth 2015).

6.2.1 Key concepts for the study of cognitive convergence

In the study of convergence, there is considerable debate over pattern-based definitions of convergence and process-based definitions (Arbuckle et al. 2014, Stayton 2015b). A process-based definition requires the convergent traits to have been produced by the same selective forces. Thus under a process-based approach to convergence, not all large brained species would necessarily be considered as ex-

amples of convergence (depending on the exact wording of the definition). Rather, *socially intelligent* taxa like the primates, cetaceans and birds (arguably) would be considered convergent as they evolved large brains for similar reasons whilst the cephalopods and hymenopterans could be considered independent evolutions of large brain size by different processes. Alternatively, a pattern-based definition of convergence could be used to consider all independent evolutions of large brains as convergent, allowing for the possibility that different processes might have created the same or similar phenotypes. In the case of cognitive evolution, process-based definitions are common, with corvid cognition (Emery and Clayton 2004), dolphin cognition (Connor 2007) and hyaena cognition (Holekamp and Benson-Amram 2017) all being described as convergent with primate cognition because of the similar social basis of the observed advanced cognitive abilities. In this study, I adopt a pattern-based approach to convergence, defining convergence simply as the independent evolution of phenotypic similarity. By studying the patterns of convergent evolution, the aim of many studies of convergence is to make inferences about the processes that may have produced the observed patterns.

Examples of convergence are numerous in the animal kingdom and there are many well established methods for identifying instances of convergence. The most simple method, beyond simply listing phylogentically distinct examples of similar traits as I have done here, is ancestral state reconstruction in which the evolutionary history of a given trait is reconstructed over a phylogeny using extant and fossil data. From this reconstruction, it is possible not only to view the distribution of the trait across a phylogeny, but to infer the historical distribution of the trait at the nodes of the tree. These nodes show us the likely phenotype of ancestral populations/species and thus allow us to infer cases of independent gains and losses of the trait in question. This method has been used to identify convergence amongst parasitic wasps driven by host pupation sites (Tschopp et al. 2013) and multiple independent losses of hindlimbs and the ability to eat large

prey in snakes (Harrington and Reeder 2017).

Alternately, the evolution of a trait (or traits) can be modelled over a phylogeny using Ornstein-Uhlenbeck models (Ingram and Mahler 2013). This approach takes a specific model of trait evolution and fits models with different number of selective regimes over the tree. A selective regime is an unspecified set of selective pressures that drive species towards a particular adaptive optimum. Thus, a change in selective regime represents a shift in the nature and/or strength of selective pressures and evolutionary processes generating the variation in the phenotype(s) being studied. Starting at the root of the tree and one selective regime, this "SURFACE" analysis adds additional selective regimes as it progresses forward in evolutionary time each time a shift occurs. Then the analysis runs backwards, from tip to root on the phylogeny, collapsing similar selective regimes together when this improves the fit of the model, as determined by Aikaike's Information Criterion (AIC). If the best fitting model identifies independent occurences of one or more regimes across the phylogeny, this is taken as evidence of convergence. For example, SURFACE analysis has been used to describe multiple instances of convergence in cranial structure amongst sauropodomorph dinosaurs (*Sauropodomorpha*) (Button et al. 2017).

These and other methods focus on identifying instances of convergence. A recently developed method takes the study of convergence a step further by quantifying the strength of convergence. The Wheatsheaf index (Arbuckle et al. 2014) quantifies the strength of convergence amongst multiple traits in a pre-defined *focal group*. The focal group is a group of species that have previously been identified or hypothesised as being convergent in some manner. The Wheatsheaf method plots all species in the study group in phenotypic space and calculates the mean Euclidean distance between the focal group species. This distance gives a measure of how tightly clustered the focal group species are in phenotypic space. To calculate the Wheatsheaf index, the distance between focal group species is compared to the mean Euclidean distance between all species. Thus, the Wheatsheaf index

is a ratio describing how similar focal group species are, compared to the entire group. A high Wheatsheaf index for a trait, or group of traits, indicates strong convergence amongst the focal group. When analysing multiple phenotypes, the Wheatsheaf index allows researchers to identify which traits are strongly convergent and which are no more similar in the focal group than across the study group as a whole. Furthermore, a very small Wheatsheaf index would indicate that the focal group is much more distantly spread in phenotypic space than would be expected, and thus would indicate divergence rather than convergence. This method has been applied to body morphology in *Anolis* lizards (Arbuckle et al. 2014), python and boa morphology (Esquerre and Keogh 2016) and social behaviour in swallows (Johnson et al. 2017).

Phylogenetically controlled comparative analyses are crucial for the study of convergence. Modern comparative analyses address biological questions whilst controlling for the statistical non-independence of data points caused by varying degrees of common ancestry throughout the sample. In the case of methods like ancestral state reconstruction and SURFACE, a phylogeny is the focus of the analysis and the trait is mapped onto the evolutionary history of the group. When calculating the Wheatsheaf index, the similarities of focal and non-focal group species are penalized for phylogenetic distance so that similar pairs of species that are very closely related are not considered the same as a pair of species with a similar phenotypic distance but a much greater phylogenetic distance (Arbuckle et al. 2014).

Here I demonstrate the application of the Wheatsheaf index, in conjunction with related methods, to investigate convergence amongst terrestrial mammalian carnivores. Finarelli and Flynn (2009) sampled brain and body sizes across 289 species (including fossil species) identifying convergent increases in encephalization in Canidae (Dogs, wolves, foxes etc.), Ursidae (bears) and Musteloidea (weasels, racoons, skunks etc.). This indicates that there were independent increases in encephalization (a measure of relative brain size) within caniform (dog-like) car-

nivores that was not matched in feliform (cat-like) carnivores (Finarelli and Flynn 2009). The authors extend their analysis to then ask whether the widely cited social brain hypothesis applies to carnivores. The social brain hypothesis holds that the cognitive demands of living and cooperating in complex social groupings create a selection pressure to increase cognitive capacity, usually indexed as relative brain size (Humphrey 1976, Dunbar 1998, 2009). In carnivorans, evidence has been advanced in favour of coevolution of sociality and relative brain size, supporting the social brain hypothesis (Perez-Barberia et al. 2007). However, Finarelli and Flynn's (2009) analysis showed that this relationship is driven by Canidae alone, suggesting that the social brain hypothesis may only account for one of the independent evolutions of large relative brain size in carnivora. Interestingly, Hyaenidae (hyaenas) do not show up as an independent evolution of encephalization in Finarelli and Flynn's (Finarelli and Flynn 2009) despite the spotted hyaena (*Crocuta crocuta*) being lauded as an example of both advanced social complexity comparable to primates and larger relative brain size than their close relatives (Holekamp and Benson-Amram 2017). This discrepancy may be due to the Hyaenidae containing only 4 species, only one of which has a relatively large brain whilst the other 3 species are very similar. This would indicate that at the family level the Hyaenidae would not be considered an independent evolution of large brain size whereas the spotted hyaena perhaps would be at the species level. Other studies of carnivora have explained the discrepancy between analyses by showing that large brains correlate to pairbonded monogamy rather than large group size (Shultz and Dunbar 2007). This mirrors findings in birds (Shultz, S. and Dunbar 2010a) and seems to demonstrate that the complexity rather than the number of social relationships is what drives the evolution of large brain size.

When instances of convergence are identified, further questions can be asked about the causes of convergence. As noted, convergent evolution of traits does not itself prove that similar evolutionary mechanisms have resulted in the observed similarities (Mahler et al. 2017). However, the strength of convergence in a

trait and related traits can provide evidence that specific evolutionary processes have acted to create the observed pattern of convergence and even to investigate how predictable such evolutionary processes may be (Arbuckle et al. 2014). For example, under the social brain hypothesis we might expect patterns of relative brain size to be very similar to patterns of convergence in social complexity across animal groups. Importantly, an adaptive hypothesis such as the social brain hypothesis would predict strong convergence in a suite of traits related to sociality.

6.3 Methods

6.3.1 Data

Data on brain and body size were gathered from primary literature, beginning with Finarelli and Flynn's (2009) dataset and adding data for a number of additional species from other sources (Isler and Schaik 2012, Lemaitre et al. 2009, Swanson et al. 2012, Damasceno et al. 2013). Data on group size, defined as the average number of individuals which regularly associate together and share a common home range (Gittleman 1986), were collected from Gittleman's papers (1982, 1986) (hereafter referred to as *social group size*) and supplemented with data taken from the species sociality descriptions from volume one of the Handbook of the Mammals of the World (Wilson and Mittermeier 2009). Life history data on dietary breadth, gestation period, inter-birth interval, mean litter size, longevity (in months), age at sexual maturity and age at weaning were taken from the PanTHERIA database (Jones et al. 2009).

6.3.2 Phylogeny

In order to control for the non-independence of data points due to shared evolutionary history, I use the updated species level supertree of carnivores (Nyakatura and Bininda-Emonds 2012). The tree used for all analyses is dated according

to the best estimates of divergence times provided by Nyakatura and Bininda-Emonds (2012).

6.3.3 Analysis

I first tested for the presence of convergence using the "SURFACE" package (Ingram and Mahler 2013) in R (R Core Team 2015). This method traces the evolution of continuous traits first forwards in evolutionary time, identifying shifts in selective regimes, and then backwards across the phylogeny to identify which regimes are similar enough to represent convergence. As well as identifying the presence of convergence, the parameters calculated by the modelling process can be used to make qualitative inferences about the nature and degree of convergence. These parameters are summarised in table 1 of Ingram and Mahler's (2013) paper describing the method. In particular, I focus on the number of regime shifts (k), the number of distinct selective regimes identified after collapsing convergent regimes (k') and the number of those shifts that are towards convergent regimes (c). Together, these parameters give a measure of the extent of convergence in the traits being analysed.

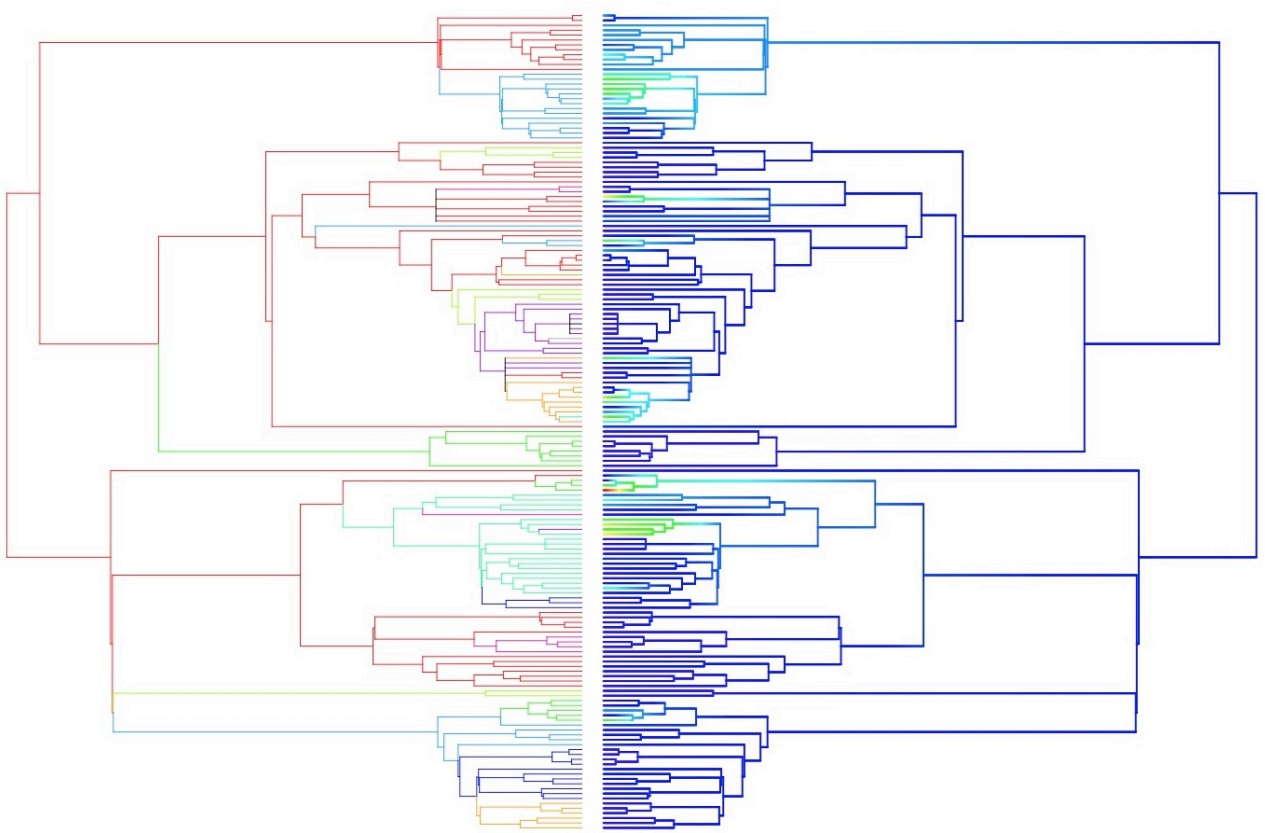

Figure 6.1: Mirrored plots of the phylogeny of carnivores, showing an ancestral state reconstruction of social group size and a SURFACE analysis of brain and body size. Smaller social groups are blue whilst larger groups are coloured red. Varying shades of green indicate medium sized groups. On the left, the branches are coloured according to unique selective regimes. It can be seen that the light blue regime has a moderately large cluster of species within Canidae that aligns well with a cluster of larger social groups on the right hand tree.

6.3.3.1 Wheatsheaf Analyses

In order to quantitatively assess the strength of convergence amongst large brained species, the Wheatsheaf index was calculated using the 'windex' package (Arbuckle and Minter 2015) in R (R Core Team 2015). Calculation of the Wheatsheaf index requires the definition of a focal group to compare the distribution of traits against the whole group. The focal group for this analysis is derived from the results of the SURFACE analysis. Since this analysis is in part concerned with the social brain hypothesis (Dunbar 1998), the focal group is selected with this in mind. SURFACE analysis of brain and body size is plotted alongside social group size data in Figure 6.1. It is clear from the social group size tree (right) that large and medium social group sizes are very rare amongst carnivores with many tips on the tree coloured blue showing small social group sizes. There is a noticeable increase in social group size within the Canidae family which corresponds with one of the selective regimes (painted onto the left tree in light blue) acting on brain and body size. This supports both the social brain hypothesis (Dunbar 1998) and Finarelli and Flynn's (2009) analysis which shows that the relationship between brain size and social group size in carnivores is driven by Canidae. The convergent regime for brain and body size identified here by SURFACE analysis (see results for full details) recurs across the tree and includes 22 species. These species that make up the focal group for subsequent analyses are *Mellivora capensis, Meles meles, Arctonyx collaris, Neofelis nebulosa, Leptailurus serval, Profelis aurata, Caracal caracal, Catopuma temminckii, Atelocynus microtis, Lycalopex culpaeus, Lycalopex gymnocercus, Cerdocyon thous, Chrysocyon brachyurus, Canis adustus, Canis mesomelas, Canis aureus, Canis latrans, Canis lupus, Canis simensis, Cuon alpinus, Lycaon pictus* and *Speothos venaticus*.

To test the prediction that Canidae and Hyaenidae will exhibit strong convergence, a second set of analyses were run with Canidae and Hyaenidae as the focal group. This grouping represents the two families of Carnivora that have

been most strongly advanced as examples of socially intelligent carnivores. The Canidae and Hyaenidae lineages used as the focal group for the second set of analyses are plotted in Figure 6.2.

For each focal group, I first calculated Wheatsheaf indices for eleven individual traits. These traits are; social group size, diet breadth, gestation period, inter-birth interval, litter size, maximum longevity, age at sexual maturity, age at weaning, brain volume, body mass and relative brain size. Relative brain size is calculated as the phylogenetic residuals from a PGLS regression of log brain volume against log body mass. These analyses investigate the strength of convergence in individual traits in each focal group. The Wheatsheaf method is also capable of analysing multiple traits in a phenotypic space. For each focal group, I calculated Wheatsheaf indices for various groupings of traits, for example social group size, diet breadth and gestation period, to investigate how tightly the focal group species cluster in n-dimensional phenotypic space where n is the number of traits being analysed.

To calculate the Wheatsheaf index (W), the mean distance in phenotypic space between species of the focal group and between species of the entire group is calculated and compared (Arbuckle et al. 2014). The Euclidean phenotypic distances are adjusted for phylogeny using the proportion of the phylogeny that each pair of species shares, taken as a pairwise distance matrix from the phylogeny. Wheatsheaf indices are also calculated without phylogenetic correction (W') to provide a measure of absolute similarity amongst focal group species. A Wheatsheaf index greater than 1 indicates that the focal group species are more similar to each other than to any random species in the group.

6.4 Results

Surface analysis of brain and body size across carnivora revealed 11 distinct regimes (k'), 9 of which are identified as convergent. Within the carnivore tree

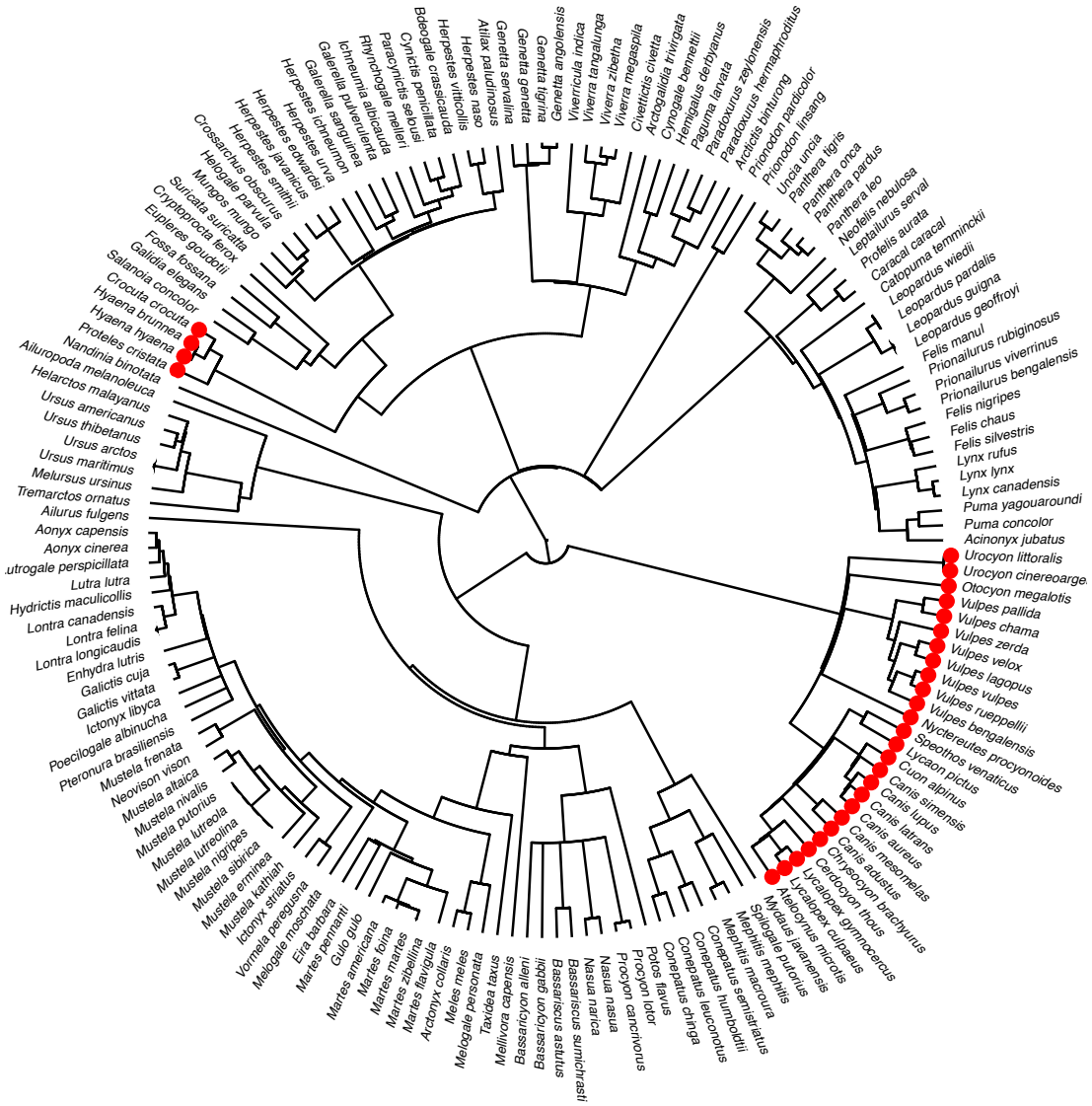

Figure 6.2: Phylogenetic tree of carnivora showing the relationship between Canidae and Hyaenidae, both labelled by filled red points at the tips of the tree. These two lineages form the focal group for the second set of Wheatsheaf method analyses.

(Figure 6.3), there are 25 shifts towards convergent regimes (c) confirming, as expected, that the evolution of brain and body size in terrestrial carnivores exhibits a high degree of convergence. This analysis indicates a high proportion of shifts towards convergent regimes. Inspecting the trait plot with adaptive optima plotted (larger filled circles) for each selective regime, it is clear the focal group under inspection here (plotted in light blue) tend to fall above the PGLS regression line describing the relationship between the traits. In particular, the placement of the adaptive optimum for the focal group's selective regime above the regression line suggests that this particular selective regime favours positive relative brain sizes (brain sizes larger than expected given the body size).

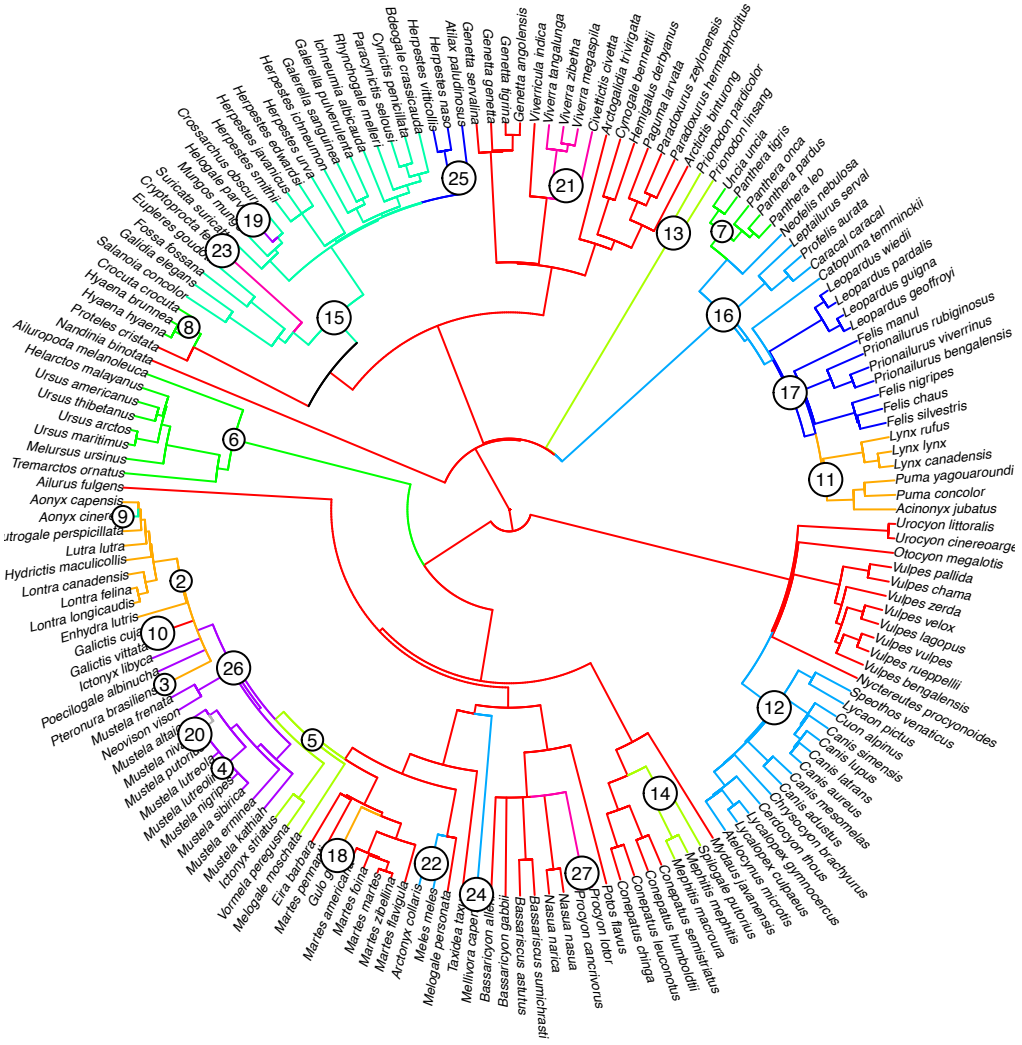

Figure 6.3: Plot of carnivore phlogenetic tree with the selective regimes identified by SURFACE analysis plotted by colour. The nodes at which regime shifts occur are numbered. The selective regime that defines the focal group in the first set of Wheatsheaf analyses is highlighted in blue. The regime shifts that lead to this focal group are numbered; 16, 12, 22 and 24.

Using the first focal group of species (listed in *Methods*), I calculated the Wheatsheaf index for eleven individual quantitative traits describing life history, diet, sociality and brain size. The results of this analysis can be seen in Table 6.1. For these individual traits, it is evident that the focal group species are not very similar in absolute brain volume (W' = 0.74) or body mass (W' = 0.54) compared to the group as a whole but they are very slightly more similar in relative brain size (W' = 1.00). When phylogeny is accounted for, relative brain size is not convergent in this selective regime (W = 0.86, p = 0.51) indicating that although

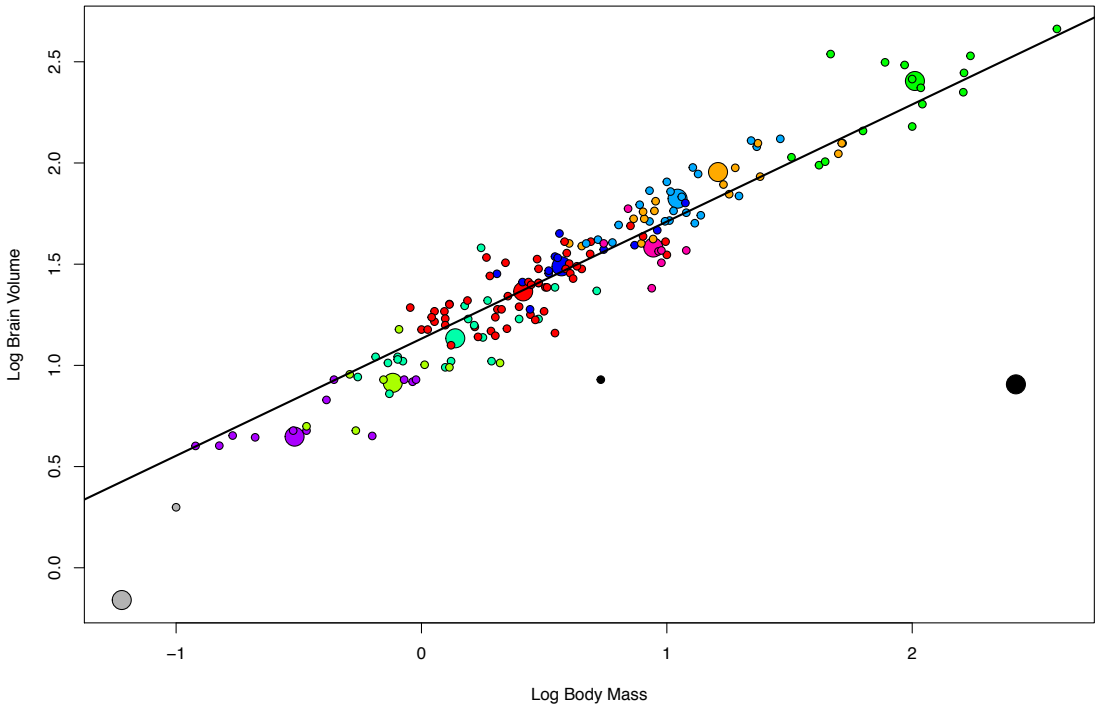

Figure 6.4: Scatter plot of Log transformed brain and body mass depicting the two dimensional phenotypic space describing these traits. Smaller points on the plot denote the position of each species in the phenotypic space. The larger points show the adaptive optima for each selective regime as calculated by SURFACE. The PGLS regression line describing the relationship between brain and body size is plotted for descriptive purposes.

the focal group is largely made up of species with positive relative brain sizes, the similarities in relative brain size are largely attributable to close phylogenetic relatedness between species. Social group sizes are also not convergent in this focal group (W = 0.79, p = 0.80) with the uncorrected index showing that focal group species do not have particularly similar social group sizes (W' = 0.83). However, focal group species are more similar in diet breadth (W' = 1.06) with a Wheatsheaf index (W = 1.13, p = 0.09) suggestive of convergence.

The Wheatsheaf indices for life history traits, listed in table 6.1, indicate signals of strong convergence in several traits. Focal group species are very similar in gestation period (W' = 1.51), longevity (W' = 1.32) and litter size (W' = 1.25). In the case of longevity, the phylogentically controlled analysis produces a lower

Wheatsheaf index (W = 1.17, p = 0.18), indicating that some of the observed similarity amongst focal group species is attributable to phylogenetic relatedness. In contrast, the Wheatsheaf index for gestation period becomes very slightly larger when correcting for phylogeny (W = 1.52, p = 0.04), indicating strong convergence in gestation period amongst focal group species. Although the age at weaning (W = 1.30, p = 0.34) appears to show signs of convergence amongst the focal group, the high p-value indicates that the bootstrapping analyses, in which the phylogeny is randomised and W is recalculated 1000 times, show that this high value for W is uncertain. In this focal group, body mass has a particularly low Wheatsheaf index (W = 0.43, p = 0.93, W' = 0.54) indicating that species within the focal group are more widely separated in body mass than carnivores as a whole. In conjunction with the high p-value, this suggests that the focal group species are actually divergent in body mass.

Table 6.1: Results of Wheatsheaf analyses including the Wheatsheaf index (W) and the uncorrected Wheatsheaf index (W') for eleven phenotypes in carnivores. W' gives a measure of how similar the focal group are in the given phenotype. W shows how similar the focal group are when the calculation is corrected for the phylogenetic non-independence of data points. Confidence intervals and the associated p-value is calculated by randomising the phylogenetic structure and calculating a possible distribution for W. Thus the p-value indicates the degree of confidence that convergence is stronger than expected.

	W	LCI	UCI	p	W'	LCI	UCI	p	W Diff
Social Group Size	0.79	0.74	0.82	0.69	0.83	0.80	0.85	0.74	-0.04
Diet Breadth	1.13	1.12	1.16	0.08	1.06	1.05	1.09	0.29	0.07
Gestation Period	1.52	1.47	1.56	0.04	1.51	1.47	1.53	0.10	0.01
Inter-birth Interval	1.02	0.99	1.03	0.51	1.02	0.99	1.03	0.54	0.00
Litter Size	1.20	1.15	1.22	0.25	1.28	1.25	1.31	0.22	-0.08
Longevity	1.17	1.14	1.20	0.18	1.35	1.32	1.38	0.14	-0.18
Age at Sexual Maturity	1.17	1.15	1.19	0.26	1.15	1.13	1.17	0.32	0.02
Age at Weaning	1.30	1.25	1.31	0.34	1.15	1.11	1.15	0.46	0.15
Brain Volume	0.62	0.60	0.63	0.82	0.74	0.71	0.74	0.86	-0.12
Body Mass	0.43	0.41	0.43	0.93	0.54	0.53	0.56	0.93	-0.11
Relative Brain Size	0.86	0.83	0.88	0.55	1.00	0.98	1.04	0.60	-0.14

I next calculated the Wheatsheaf indices for various combinations of traits, testing the strength of convergence across multiple traits. These analyses are summarised in Table 6.2. From these results it is clear that in combination, social group size and diet breadth exhibit relatively strong convergence (W = 1.16, p

= 0.08). Few other combinations of traits that include social group size have W indices greater than 1, despite some combinations having W' values greater than 1 such as social group size, age at sexual maturity and interbirth interval (W' = 1.06), indicating greater similarity among the focal group species compared to all carnivores. Notably, excluding social group size from the analysis produces a stronger signal of convergence in each combination. This is most noticeable in the case of diet breadth, age at sexual maturity and interbirth interval, in which focal group species are much more similar to each other than randomly selected species (W' = 2.004) and the Wheatsheaf index indicates strong convergence (W = 1.48, p = 0.015). In these groupings of traits, there are numerous grouopings with small Wheatsheaf indices. For example, the focal group appear to be divergent in the trait space of social group size, age at sexual maturity, age at weaning and inter-birth interval (W = 0.616, p = 0.963). In the trait spaces that are defined by social group size, diet breadth and various life history variables (rows 6 through 9 in table 6.2), the Wheatsheaf indices and p-values are all indicative of divergence, suggesting that the focal group are more distantly clustered in trait space than would be expected. The same is true of brain volume, body mass and social group size (W = 0.551, p = 0.933), suggesting that the focal group species exhibit divergence in these traits.

Table 6.2: Results of Wheatsheaf analyses including the Wheatsheaf index (W) and the uncorrected Wheatsheaf index (W') for various groupings of phenotypes in carnivores. W' gives a measure of how similar the focal group are in the given phenotype. W shows how similar the focal group are when the calculation is corrected for the phylogenetic non-independence of data points. Confidence intervals and the associated p-value is calculated by randomising the phylogenetic structure and calculating a possible distribution for W. Thus the p-value indicates the degree of confidence that convergence is stronger than expected.

	W	LCI	UCI	p	W'	LCI	UCI	p	W Diff
Social Group Size, Diet Breadth	1.164	1.142	1.197	0.081	1.094	1.068	1.146	0.195	0.070
Social Group Size, Age at Sexual Maturity, Age at Weaning, Interbirth Interval	0.616	0.579	0.672	0.963	0.747	0.723	0.778	0.964	-0.130
Social Group Size, Age at Sexual Maturity, Age at Weaning	0.721	0.677	0.762	0.789	1.018	0.985	1.132	0.642	-0.297
Social Group Size, Age at Sexual Maturity, Interbirth Interval	0.878	0.830	0.931	0.584	1.059	1.021	1.179	0.522	-0.182
Social Group Size, Interbirth Interval	0.810	0.775	0.842	0.727	0.915	0.894	0.930	0.710	-0.105
Social Group Size, Age at Sexual Maturity, Age at Weaning, Interbirth Interval, Diet Breadth	0.661	0.610	0.679	0.906	0.768	0.733	0.775	0.944	-0.106
Social Group Size, Age at Sexual Maturity, Age at Weaning, Diet Breadth	0.615	0.574	0.625	0.908	0.859	0.823	0.869	0.852	-0.243
Social Group Size, Age at Sexual Maturity, Interbirth Interval, Diet Breadth	0.496	0.469	0.517	0.997	0.588	0.569	0.621	1.000	-0.091
Social Group Size, Interbirth Interval, Diet Breadth	0.661	0.621	0.693	0.895	0.759	0.735	0.778	0.875	-0.098
Age at Sexual Maturity, Age at Weaning, Interbirth Interval, Diet Breadth	1.064	1.006	1.075	0.234	1.114	1.068	1.121	0.410	-0.050
Age at Sexual Maturity, Age at Weaning, Diet Breadth	1.085	1.021	1.146	0.133	1.341	1.290	1.378	0.150	-0.257
Age at Sexual Maturity, Interbirth Interval, Diet Breadth	1.480	1.396	1.523	0.015	2.004	1.943	2.051	0.009	-0.524
Interbirth Interval, Diet Breadth	0.945	0.917	0.983	0.425	1.154	1.132	1.174	0.456	-0.209
Brain Volume, Body Mass	0.601	0.574	0.610	0.867	0.722	0.696	0.738	0.874	-0.121
Brain Volume, Body Mass, Social Group Size	0.551	0.521	0.562	0.933	0.720	0.692	0.726	0.872	-0.169
Relative Brain Size, Social Group Size	0.484	0.460	0.488	0.906	0.565	0.545	0.568	0.907	-0.081

The results of Wheatsheaf analyses using Canidae and Hyaenidae as the focal group are summarised in tables 6.3 and 6.4. Age at weaning (W = 1.95, p = 0.07), gestation period (W = 1.37, p = 0.12) and age at sexual maturity (W = 1.35, p = 0.09) are strongly convergent as single variables. Whilst both absolute brain volume and body mass have Wheatsheaf indices above 1, suggesting convergence

in body size but not necessarily relative brain size which is not strongly convergent (W = 0.94, p = 0.68). Social group size exhibits no evidence of strong convergence amongst canids and hyaenas (W = 0.89, p = 0.69).

Table 6.3: Results of Wheatsheaf analyses including the Wheatsheaf index (W) and the uncorrected Wheatsheaf index (W') for eleven phenotypes in carnivores. W' gives a measure of how similar the focal group are in the given phenotype. W shows how similar the focal group are when the calculation is corrected for the phylogenetic non-independence of data points. Confidence intervals and the associated p-value is calculated by randomising the phylogenetic structure and calculating a possible distribution for W. Thus the p-value indicates the degree of confidence that convergence is stronger than expected. The focal group for this analysis is made up of the two families; Canidae and Hyaenidae.

	W	LCI	UCI	p	W'	LCI	UCI	p	W Diff
Social Group Size	0.889	0.857	0.914	0.694	0.802	0.775	0.826	0.836	0.087
Diet Breadth	1.040	1.030	1.043	0.256	1.007	1.007	1.013	0.686	0.033
Gestation Period	1.374	1.343	1.397	0.124	1.194	1.169	1.199	0.254	0.180
Inter-birth Interval	1.030	1.000	1.038	0.606	0.875	0.850	0.880	0.768	0.155
Litter Size	1.302	1.269	1.342	0.103	1.239	1.219	1.266	0.182	0.063
Longevity	1.128	1.105	1.156	0.356	1.035	1.016	1.062	0.508	0.093
Age at Sexual Maturity	1.350	1.325	1.380	0.087	1.233	1.213	1.260	0.138	0.117
Age at Weaning	1.955	1.899	1.976	0.074	1.772	1.728	1.782	0.092	0.182
Brain Volume	1.207	1.165	1.221	0.309	1.205	1.163	1.214	0.344	0.002
Body Mass	1.055	1.018	1.062	0.539	1.038	1.000	1.043	0.565	0.017
Relative Brain Size	0.935	0.917	0.959	0.678	0.929	0.915	0.953	0.778	0.007

As combined traits (Table 6.4), very few combinations show signs of strong convergence. Amongst the exceptions are social group size, age at maturity and interbirth interval (W = 1.30, p = 0.10) and age at maturity, interbirth interval and diet breadth (W = 1.22, p = 0.06). Both combinations of traits exhibit relatively strong convergence. Interestingly, Canidae and Hyaenidae cluster quite closely in phenotypic space when plotting brain size, body size and social group size together (W' = 1.22), indicating that these species more closely resemble each other. When phylogeny is accounted for, the signal of convergence disappears with the p-value indicating that the value of W is highly uncertain (W = 1.096, p = 0.50), possibly indicating that the similarity observed with W' is largely due to similarity amongst the Canidae which is then penalised for phylogenetic distance. Critically, when relative brain size and social group size are combined to create a 2-dimensional trait space, Canidae and Hyaenidae cluster

together closely (W' = 1.782). The strength of convergence appears high but the relatively high p-value indicates a low degree of confidence in the W index (W = 1.59, p = 0.24), indicating that no strong conclusions can be drawn from this result. This trait space is plotted in Figure 6.5, showing that Canidae and Hyaenidae (plotted in red) are clustered more tightly than expected if there were no convergence. This plot is not intended to reveal a correlation or lack or correlation but rather the clustering of the focal group (plotted in red) compared to the group as a whole. Although there is no evidence of divergence in the univariate analyses in Canidae and Hyaenidae, the two lineages do appear to be divergent in the trait space defined by age at sexual maturity, age at weaning, interbirth interval and diet breadth (W = 0.779, p = 0.978).

Table 6.4: Results of Wheatsheaf analyses including the Wheatsheaf index (W) and the uncorrected Wheatsheaf index (W') for various groupings of phenotypes in carnivores. W' gives a measure of how similar the focal group are in the given phenotype. W shows how similar the focal group are when the calculation is corrected for the phylogenetic non-independence of data points. Confidence intervals and the associated p-value is calculated by randomising the phylogenetic structure and calculating a possible distribution for W. Thus the p-value indicates the degree of confidence that convergence is stronger than expected. The focal group for this analysis is made up of the two families; Canidae and Hyaenidae.

	W	LCI	UCI	p	W'	LCI	UCI	p	W Diff
Social Group Size, Diet Breadth	0.950	0.929	0.973	0.989	0.934	0.923	0.961	0.998	0.015
Social Group Size, Age at Sexual Maturity, Age at Weaning, Interbirth Interval	0.869	0.844	0.907	0.852	0.846	0.825	0.874	0.894	0.023
Social Group Size, Age at Sexual Maturity, Age at Weaning	1.008	0.978	1.050	0.523	1.008	0.976	1.075	0.559	0.000
Social Group Size, Age at Sexual Maturity, Interbirth Interval	1.301	1.254	1.369	0.103	1.298	1.251	1.399	0.122	0.003
Social Group Size, Interbirth Interval	0.956	0.936	0.974	0.606	0.975	0.960	0.979	0.583	-0.019
Social Group Size, Age at Sexual Maturity, Age at Weaning, Interbirth Interval, Diet Breadth	0.910	0.867	1.063	0.777	0.847	0.810	0.947	0.883	0.064
Social Group Size, Age at Sexual Maturity, Age at Weaning, Diet Breadth	0.899	0.865	0.936	0.796	0.912	0.880	0.980	0.797	-0.013
Social Group Size, Age at Sexual Maturity, Interbirth Interval, Diet Breadth	0.789	0.760	0.862	0.918	0.801	0.776	0.855	0.935	-0.011
Social Group Size, Interbirth Interval, Diet Breadth	1.024	0.988	1.062	0.522	0.990	0.955	1.020	0.557	0.034
Age at Sexual Maturity, Age at Weaning, Interbirth Interval, Diet Breadth	0.779	0.747	0.791	0.987	0.819	0.789	0.824	0.988	-0.040
Age at Sexual Maturity, Age at Weaning, Diet Breadth	0.897	0.857	0.946	0.683	0.946	0.914	0.985	0.736	-0.050
Age at Sexual Maturity, Interbirth Interval, Diet Breadth	1.222	1.179	1.239	0.064	1.332	1.300	1.353	0.059	-0.110
Interbirth Interval, Diet Breadth	1.090	1.070	1.114	0.372	1.177	1.154	1.200	0.372	-0.087
Brain Volume, Body Mass	1.107	1.067	1.153	0.416	1.107	1.065	1.126	0.437	0.000
Brain Volume, Body Mass, Social Group Size	1.096	1.052	1.135	0.436	1.224	1.176	1.257	0.325	-0.128
Relative Brain Size, Social Group Size	1.589	1.492	1.621	0.239	1.782	1.667	1.821	0.182	-0.193

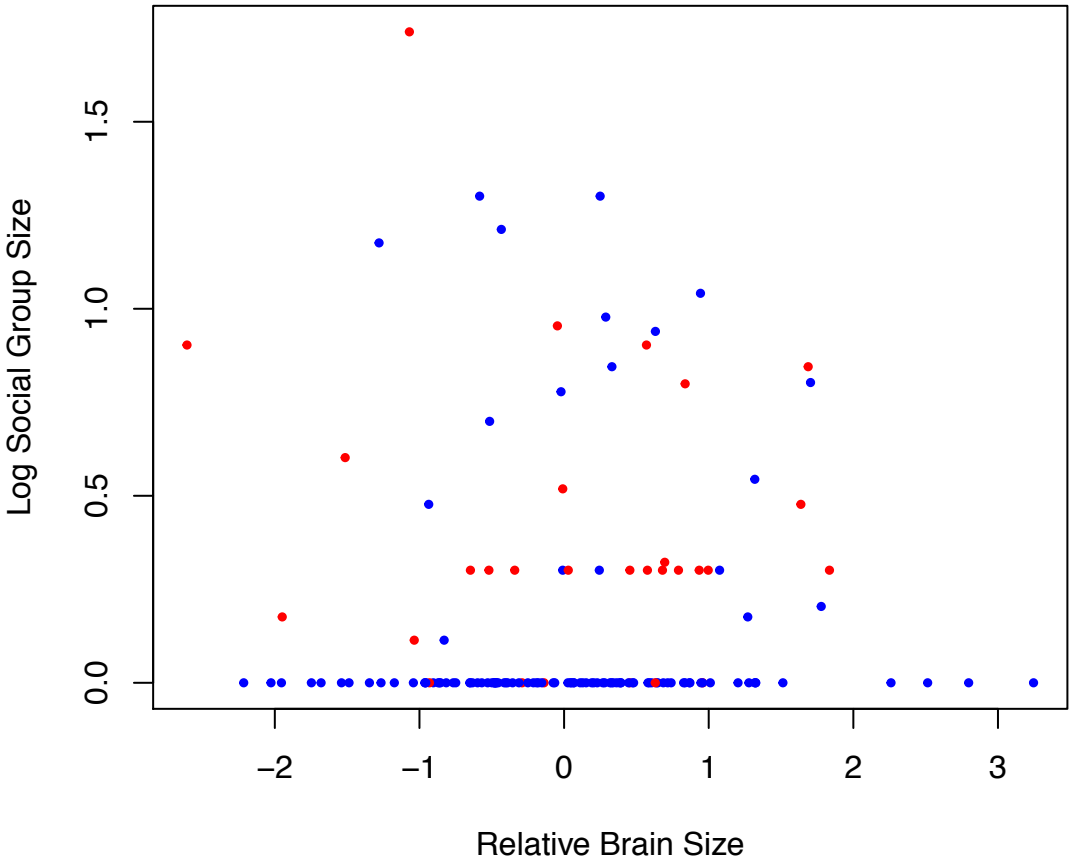

Figure 6.5: Scatter plot of relative brain size and social group size depicting focal group species in red and non-focal group species in blue.

6.5 Discussion

The analyses presented here show a number of convergent regimes in carnivore brain and body size. Large brain sizes, relative to body mass, have evolved multiple times in terrestrial carnivores as shown in figure 6.3. This is in agreement with previous research that identified multiple independent shifts in relative brain size in terrestrial carnivores (Finarelli and Flynn 2009). Previous research has indicated that in carnivores, the only lineage that conforms to the predictions of the social brain hypothesis is Canidae (Finarelli and Flynn 2009), although it should be noted that at least one species of Hyaenidae, *Crocuta crocuta* has been advanced as another example of a socially intelligent species (Holekamp and Benson-Amram 2017). Here I find no evidence of strong convergence in

social grouping, either alone or in combination with other traits (except diet breadth), amongst species that occupy the same selective regime as the highly social Canidae. Thus the results of this analysis initially are not supportive of the social brain hypothesis. Finarelli and Flynn's (2009) study of brain size and sociality in carnivores showed that the extent to which carnivores conform to the expectations of the social brain hypothesis is limited to one family (Canidae) and in light of this, I would not expect to find that large social group sizes and brain sizes have convergently evolved within carnivora. Furthermore, the finding that pairbonded monogamy is correlated to large brain size evolution in carnivores (Shultz and Dunbar 2007) demonstrates that under the social brain hypothesis, we do not expect that large social groups and brain sizes will correlate outisde of primates (Dunbar 1992) and cetaceans (Fox et al. {2017}). Therefore the findings presented here do not necessarily contradict the social brain hypothesis as I have not tested the prediction that monogamy is related to brain size. Rather, these analyses search for patterns of convergent evolution in continuous traits across carnivores.

Species that occupy the same selective regime of brain and body size as a highly social lineage within Canidae (depicted in light blue in Figure 6.1), by the Wheatsheaf measure, do not exhibit convergence in social group size or relative brain size. These species are more similar in a number of life history traits such as gestation, weaning age and litter size which all show varying strengths of convergence. This pattern of convergence suggests that the regimes identified in the SURFACE analysis describe selective pressures that are acting more strongly on life history than social or cognitive aspects of the focal group species. It should be noted that although the Wheatsheaf index clearly indicates that the focal group species show strong convergence in gestation period and weaning age, it does not necessarily indicate a significant difference in mean phenotypic value in either direction. A high Wheatsheaf index indicates that focal group species are more similar to each other than to any randomly selected species. The finding that

within this focal group, social group size and dietary breadth together exhibit strong covergent evolution is intriguing. However, it is only when social group size is excluded from the Whetasheaf analyses including life history variables that the focal group shows strong convergence. This suggests (as also suggested by the univariate analyses) that dietary breadth is under convergent selection pressure in the focal group much more than social group size.

A link between brain size and diet is not novel. Although previous research found no evidence that dietary quality correlates with brain size in platyrrhines (new world monkeys) (Allen and Kay 2012), DeCasien and collegues (2017) analysed a larger sample of primates than previous studies to show that frugivores (fruit eaters) have larger brains than folivores (leaf eaters). In another example of ecology and diet influencing brain size, large relative brain size in marsupials is attributed to living in stable, benign environments in which nutritional pressures are relaxed, allowing metabolically expensive brain tissue to expand without the need for a behavioural selection pressure driving the increase in size (Weisbecker et al. 2015).

To more explicitly investigate the social brain hypothesis in carnivores, I also calculated Wheatsheaf indices with two carnivore families, Canidae and Hyaenidae as the focal group. Both of these families contain large brained, highly social species as well as some less social and even solitary species. It would be inappropriate to make strong claims in either direction about the underlying evolutionary mechanisms that produce the results calculated in this analysis. As noted, convergence is a pattern rather than a process (Arbuckle et al. 2014, Stayton 2015b) and therefore the presence or absence of a particular pattern does not necessarily imply a particular adaptive process (eg. the evolution of the social brain) has produced the pattern observed. However, convergence can also be thought of as the study of the degree to which evolution can be predicted. For example, under the social brain hypothesis, one would predict that species that evolved to have complex social bonds would have a number of phenotypes that are very

similar precisely because of the evolutionary mechanisms acting to produce the observed distribution of trait values. This analysis fails to find such convergence in Canidae and Hyaenidae, thus failing to support the predictions of the social brain hypothesis. Canidae have long been recognised as a highly social group and this is supported by the reconstruction of social group size shown in Figure 6.1 (See *Methods*) in which there is a clustering of medium to large social group sizes within the family. As mentioned throughout this chapter, it has been shown that the Canidae family conform to the predictions of the social brain hypothesis (Finarelli and Flynn 2009). Within Hyaenidae, there is actually considerable variation between the four species in terms of social group size (ranging from 1 to 55). Hyaenidae, particularly the spotted hyaena (*Crocuta crocuta*), have been advanced as an example of a lineage in which the social brain hypothesis explains the evolution of large brains (Holekamp and Benson-Amram 2017). Although both lineages seem to cluster relatively closely in the two-dimensional phenotypic space created by relative brain size and social group size (see table 6.4, Figure 6.5), the two taxa are not strongly convergent in these traits.

Vital to the interpretation of Wheatsheaf indices is the selection of the focal group. In this study, I have demonstrated two different approaches to selecting a focal group. Firstly, I ran a SURFACE analysis to identify convergent regimes in brain and body mass and chose one from amongst the nine convergent regimes modelled. This approach gave a focal group of 22 species from four phylogenetically distinct groupings (Figure 6.3). The chosen convergent regime was selected specifically because it aligned with a trait of interest (Figure 6.1) in one grouping on the phylogeny. This exploratory approach allows researchers to investigate the strength of convergence in many traits within a group of species that has been identified as exhibiting convergence in a trait or traits of interest. For the second set of Wheatsheaf analyses, I selected the focal group based on the social brain hypothesis (Dunbar 1998, 2009). Selecting a focal group in this manner allows researchers to test the predictability of evolution as well as identify which traits

are strongly convergent in the niche of interest. It is possible to select a focal group using traits themselves, for example one possible focal group could include all species above some threshold of relative brain size. However, this approach risks biasing the analysis as species may be included or excluded arbitrarily. For this reason, it is important to select a focal group that has either been postively identified as exhibiting convergence (by SURFACE or other methods) or has been hypothesised to be convergent as in the case of Canidae and Hyaenidae (Finarelli and Flynn 2009, Holekamp et al. 2007, Holekamp and Benson-Amram 2017).

Traditionally, the social brain hypothesis has relied on studies that show postive relationships between social group size and brain size (Dunbar 1992). Likewise, studies of convergence in cognition/brain size and specifically claims of lineages converging on social intelligence have predominantly taken the form of listing pylogentically distant examples of similar traits (Holekamp and Benson-Amram 2017, Roth 2015, Emery and Clayton 2004). This study demonstrates the usage of the Wheatsheaf index (Arbuckle et al. 2014), in conjunction with SURFACE (Ingram and Mahler 2013) to conduct a phylogenetically informed, statistical study of convergence in traits of interest in the studies of cognition and social intelligence. I provide evidence that across carnivora, patterns of convergence in brain and body size do not necessarily conform to the expectations of the social brain hypothesis, indicating that perhaps other selective pressures have acted on brain and body size across carnivora. However it should be noted that monogamy was not included in this analysis and so this study does not present a direct test of the social brain hypothesis.

7 Conclusions

7.1 Directions for Future Research

Throughout this thesis I have used a number of different modern statistical methods to investigate outstanding questions about the evolution of brain size and cognition. In Chapter three, I identified a non-social causal factor in primate brain evolution (the transition to a terrestrial niche), contradicting the current consensus view that the social brain hypothesis explains the expansion of brain size in primates. Contrary to another recent study (DeCasien et al. 2017), I did find support for a significant positive relationship between social group size and cognitive ability. This contributes to a complex picture in which an exclusively social interpretation of primate brain evolution is not supported as several factors appear to have influenced brain size. Future research should aim to disentangle the complex relationships between the multiple determinants of cognitive abilities in primates.

In Chapter four, I use the recently developed method of phylogenetic path analysis (Gonzalez-Voyer and Hardenberg 2014) to address a longstanding controversy in cetacean brain evolution. By using the powerful method of path analysis, I was able to advance the debate over the thermogenesis hypothesis by clearly demonstrating that neither the range nor the minimum habitat temperatures predicted brain size in cetaceans. I also demonstrated a weak relationship between social structure and brain size, appearing to support the social brain hypothesis. This relationship is much weaker than comparable relationships in primates and future research should aim to further investigate the link between sociality and brain size in cetaceans. This will require detailed data on the social lives of cetaceans which in many cases are difficult to observe. In fact, the difficulty in observing the behaviour of many cetaceans has made large scale comparative analyses of sociality across the groups extremely difficult.

My analysis of the thermogenesis hypothesis is more complete than previous attempts but future research should not yet abandon the hypothesis. If there is some merit to the hypothesis, a relationship between habitat temperature and brain size may be observable in the highly studied killer whale (*Orcinus orca*). Killer whales have an extremely broad geographic range but the population is split into ecomorphs, each of which occupies different waters and even has different behavioural specialisations (Wilson and Mittermeier 2014). A detailed study of intraspecific variation in brain size and behaviour between the killer whale populations would provide an opportunity to evaluate the possible effect of living in cold waters compared to more temperate waters.

Chapter five presents evidence that relative brain size does not differ significantly between hosts and non-hosts of avian brood parasites. This conclusion leads to one of two explanations. The first is that hosts and non-hosts do not differ in cognitive ability and thus a difference in brain size between the two groups would not be expected. However, the extreme costs of parasitism place strong pressures on hosts and so it seems likely that natural selection would have favoured advanced cognitive abilities to mitigate those costs. The second possible conclusion is that if there is a difference in cognitive ability between hosts and non-hosts, it is not reflected in the brain sizes of either group, possibly because of constraints on development imposed by the pressures of the host-parasite coevolutionary arms race. Future research into avian cognitive evolution should aim to determine the cognitive abilities of brood parasite hosts and potentially investigate how advanced cognitive abilites can arise without increases in brain size.

Finally, Chapter six demonstrates the application of modern statistical methods to study convergent evolution. The study of cognition has traditionally focused on specific groups of animals, with comparisons between groups being qualitative (eg. Holekamp and Benson-Amram 2017, Emery and Clayton 2004, Roth 2015). Methods like SURFACE (Ingram and Mahler 2013) and the Wheatsheaf index (Arbuckle et al. 2014) should allow future research to evaluate the strength of

convergence between groups of interest. Furthermore, the Wheatsheaf index will allow quantitative evaluation of many phenotypic traits and how similar they are in cognitively complex species. This kind of analysis will allow researchers to answer questions about broad evolutionary processes influencing brain size evolution across many taxa.

7.2 Challenges in the Study of Cognition

The study of cognitive abilities in animals suffers from a number of methodological concerns. Chief amongst these concerns is the fact that the overwhelming majority of studies into animal cognition use relative brain size as an indirect measure of cognitive ability (Healy and Rowe 2007). In Chapter three, I used behavioural markers of cognitive complexity rather than brain size to analyse primate cognitive evolution, building on previous work to investigate cognition more directly (Reader and Laland 2002, Reader et al. 2011). However, throughout the rest of the work presented here, I revert to using brain size. The principal reason for this difference in methodology is that behavioural data of the quality and taxonomic breadth of those available in primates are not readily available in other animal groups. In birds, reports of behavioural innovation have been gathered and shown to be related to brain size (Overington et al. 2009, 2011). In carnivores and cetaceans, descriptions of behaviours such as tool use and innovation are limited to captive studies (Benson-Amram et al. 2016, Gunturkun 2014) and a few heavily studied species in the wild (Connor and Krützen 2015, Smolker et al. 1997, Holekamp and Benson-Amram 2017). Despite concerns being raised about the number of studies using relative brain size (Healy and Rowe 2007), several studies have clearly demonstrated relationships between brain size and cognitively complex behaviours (Byrne and Corp 2004, Joffe and Dunbar 1997, Pawlowski et al. 1998, Kudo and Dunbar 2001, Reader and Laland 2002, Lefebvre et al. 2004, Lindenfors 2005, Reader et al. 2011, Overington et al. 2009, Benson-Amram et al. 2016). These studies validate the use of brain size as a

metric of cognitive ability.

However, the findings presented in Chapter five present a potential challenge to the consensus view that brain size is a reliable indicator of cognitive ability. I provided a potential explanation for the lack of a difference in brain size between hosts and non-hosts with the suggestion that developmental constraints imposed upon the hosts, limit the expansion of brain tissue. This suggests an example in which cognitive abilities may not be reliably inferred from brain size alone. The alternative interpretation, that hosts and non-hosts do not differ in cognitive ability, must also be considered but the evolutionary pressures acting on host cognition make this unlikely (See Chapter five for details). The possibility that brain size may not always be a reliable metric of cognitive ability is something that must be considered when studying lineages in which there may be constraints on brain size.

7.3 Concluding Remarks

The comparative method has been and will continue to be a powerful tool in the study of cognition. The four studies presented here show that a variety of ecological and social factors can influence brain evolution in different ways. The future of comparative cognition research should aim to expand beyond the natural focus on primates to explore the similarities and differences in the evolutionary processes that give rise to the variation in brain size and cognitive ability.

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1 Appendix

1.1 Cetacean Sensitivity Analysis

Intermediate social classifications were rounded up and down and the analysis was rerun to test the sensitivity of the results to the uncertainty in the social structure data.

Range

When the social complexity data is rounded down, biasing the data towards more simple social structures, the combined hypothesis is still favoured over all other models (Table 1.1). Similarly, rounding the social data up, biasing it towards increased complexity in the social lives of cetaceans, shows that the combined model still has the greatest degree of statistical support (Table 1.2).

Table 1.1: Results of phylogenetically controlled path analysis, with social complexity data rounded down, of the social brain hypothesis, thermogenesis hypothesis, combined hypothesis and a null hypothesis using Fisher's C and CICc to order the hypotheses by degree of statistical support.

Model	C statistic	p-value	CICc
Combined	0.272	0.873	24.479
Thermogenesis	6.033	0.197	26.833
Social Brain	8.080	0.089	28.880
Null	14.579	0.001	32.192

Table 1.2: Results of phylogenetically controlled path analysis, with social complexity data rounded up, of the social brain hypothesis, thermogenesis hypothesis, combined hypothesis and a null hypothesis using Fisher's C and CICc to order the hypotheses by degree of statistical support.

Model	C statistic	p-value	CICc
Combined	4.152	0.125	28.359
Social Brain	9.960	0.041	30.760
Thermogenesis	12.961	0.012	33.761
Null	22.865	0.000	40.478

Figure 1.1 shows both supplementary analyses depicted either side of the original analysis of the unaltered data. The regression coefficients depicted vary only

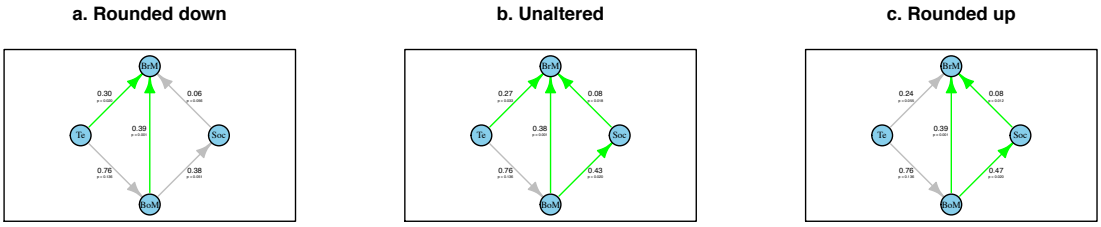

Figure 1.1: Path diagrams including PGLS regression models showing the magnitude and significance of causal relationships in three analyses of the same model. These analyses take the intermediate classifications within the social complexity data and round them down (a.), leave them unaltered (b.) and round them up (c.). Statistically significant causal relationships are shown in green and non-significant relationships are depicted in grey.

marginally between the three models, as do the associated p-values. The p-value associated with the key relationship of habitat temperature and brain size varies between 0.020 and 0.055 between the three models. Similarly, the p-value associated with the sociality and brain size relationship varies between 0.056 and 0.012. These small changes are mirrored in the regression coefficients and indicate that the overall interpretation of these analyses is not unduly vulnerable to the uncertainty in the data.

Table 1.3 shows the results of the 3 PGLS models from the causal model depicted in Figure 1.1a. in which social complexity data were rounded down. Table 1.4 contains the same models but with social complexity data rounded up as in Figure 1.1c.

Table 1.3: Results of PGLS models describing the hypothesised causal relationships between brain size, body size, sociality and habitat temperature range with social complexity data rounded down.

Outcome	Predictor	β	Std. Error	p-value	λ
Brain Mass	Body Mass	0.392	0.04	0	0.888
	Temperature Range	0.299	0.123	0.02	
	Sociality	0.058	0.029	0.056	
Sociality	Body Mass	0.376	0.187	0.051	1
Body Mass	Temperature Range	0.764	0.502	0.136	0.964

Table 1.4: Results of PGLS models describing the hypothesised causal relationships between brain size, body size, sociality and habitat temperature range with social complexity data rounded up.

Outcome	Predictor	β	Std. Error	p-value	λ
Brain Mass	Body Mass	0.386	0.037	0	0.861
	Temperature Range	0.242	0.122	0.055	
	Sociality	0.083	0.031	0.012	
Sociality	Body Mass	0.468	0.186	0.016	0.905
Body Mass	Temperature Range	0.764	0.502	0.136	0.964

Minimum Habitat Temperature

Table 1.5 shows the results of pathway model evalution when social complexity data is rounded down. The results show that the social brain model and the combined model are still jointly favoured. As in the main analysis (Chapter 4), the social brain model is slightly favoured but the difference in CICc of less than 2 indicates no significant difference the models in explanatory power. When the social data is rounded up (table 1.6), the relative explanatory power of the models is unchanged with both the social and combined models being favoured and the null model and the thermogenesis model being rejected.

Table 1.5: Results of phylogenetically controlled path analysis, with social complexity data rounded down, of the social brain hypothesis, thermogenesis hypothesis, combined hypothesis and a null hypothesis using Fisher's C and CICc to order the hypotheses by degree of statistical support.

Model	C statistic	p-value	CICc
Social Brain	4.171	0.383	24.971
Combined	1.456	0.483	25.663
Thermogenesis	7.363	0.118	28.163
Null	10.714	0.005	28.327

Table 1.6: Results of phylogenetically controlled path analysis, with social complexity data rounded up, of the social brain hypothesis, thermogenesis hypothesis, combined hypothesis and a null hypothesis using Fisher's C and CICc to order the hypotheses by degree of statistical support.

Model	C statistic	p-value	CICc
Social Brain	4.302	0.367	25.102
Combined	1.322	0.516	25.529
Null	14.985	0.001	32.598
Thermogenesis	11.894	0.018	32.694

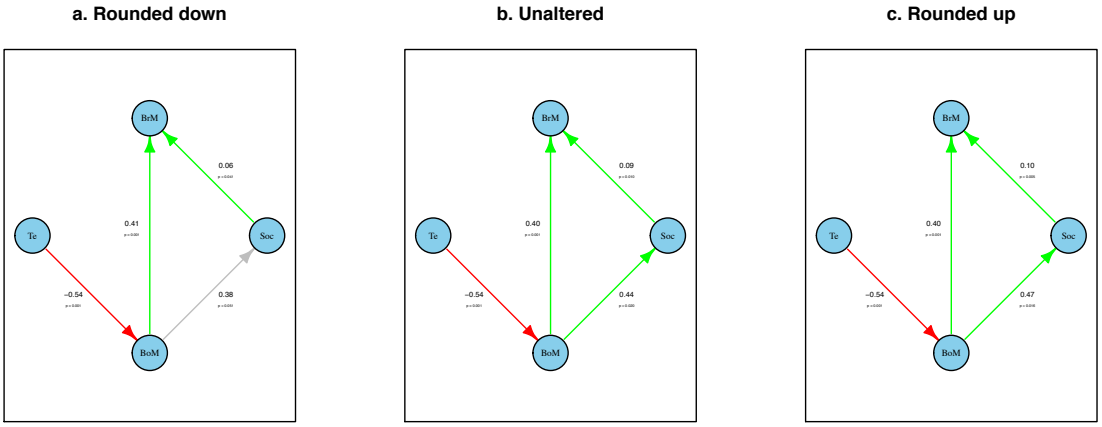

Figure 1.2: Path diagrams including PGLS regression models showing the magnitude and significance of causal relationships in three analyses of the social brain model using minimum habitat temperature. These analyses take the intermediate classifications within the social complexity data and round them down (a.), leave them unaltered (b.) and round them up (c.). Statistically significant causal relationships are shown in green and non-significant relationships are depicted in grey.

Figure 1.2 shows the causal relationships between minimum habitat temperature, social structure, body mass and brain size in the orginal analysis (1.2b) and in both cases where the social data has been rounded down (1.2a) and up (1.2c). Figure 1.3 shows the analyses of the combined model in each of the 3 cases. In both cases there are no large changes in effect size across when sociality is rounded up or down. When sociality is rounded down, the influence of sociality on brain size becomes narrowly non-significant ($p = 0.052$) in the combined model but the relatively small change in p-value is to be expected when biasing the data towards simple social structures.

Tables 1.7 through 1.10 contain the results of PGLS models detailing the reanalysis of both the social and combined models when social structure data is rounded up and down.

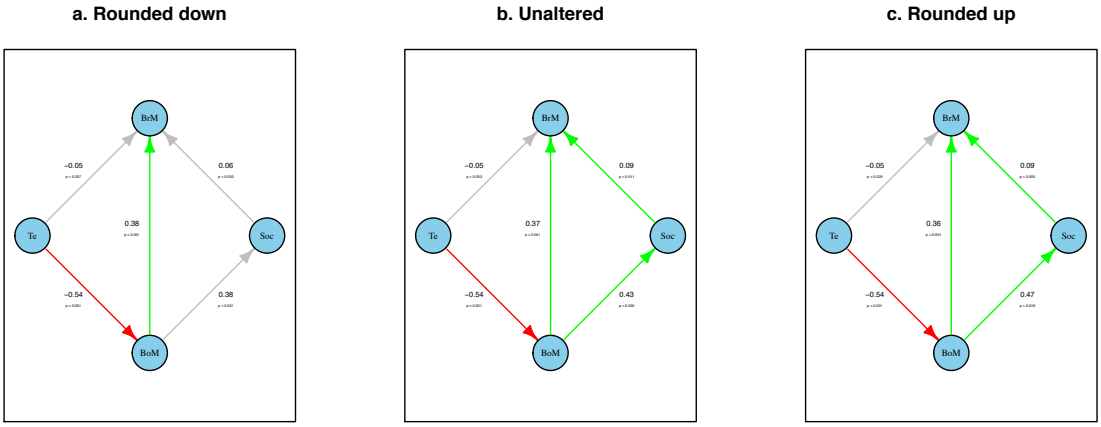

Figure 1.3: Path diagrams including PGLS regression models showing the magnitude and significance of causal relationships in three analyses of the combined model using minimum habitat temperature. These analyses take the intermediate classifications within the social complexity data and round them down (a.), leave them unaltered (b.) and round them up (c.). Statistically significant causal relationships are shown in green and non-significant relationships are depicted in grey.

Table 1.7: Results of PGLS models describing the hypothesised causal relationships between brain size, body size, sociality and minimum habitat temperature under the social brain hypothesis with social complexity data rounded down.

Outcome	Predictor	β	Std. Error	p-value	λ
Brain Mass	Body Mass	0.410	0.041	< 0.001	0.863
	Sociality	0.065	0.031	0.044	
Sociality	Body Mass	0.376	0.187	0.051	1.000
Body Mass	Minimum Temperature	-0.543	0.124	< 0.001	0.913

Table 1.8: Results of PGLS models describing the hypothesised causal relationships between brain size, body size, sociality and minimum habitat temperature under the social brain hypothesis with social complexity data rounded up.

Outcome	Predictor	β	Std. Error	p-value	λ
Brain Mass	Body Mass	0.399	0.039	< 0.001	0.873
	Sociality	0.096	0.032	0.005	
Sociality	Body Mass	0.468	0.186	0.016	0.905
Body Mass	Temperature Range	-0.543	0.124	< 0.001	0.913

Table 1.9: Results of PGLS models describing the hypothesised causal relationships between brain size, body size, sociality and habitat temperature range under the combined model with social complexity data rounded down.

Outcome	Predictor	β	Std. Error	p-value	λ
Brain Mass	Body Mass	0.377	0.048	< 0.001	0.836
	Temperature Range	-0.053	0.046	0.257	
	Sociality	0.062	0.031	0.052	
Sociality	Body Mass	0.376	0.186	0.051	1.000
Body Mass	Temperature Range	-0.543	0.124	< 0.001	0.913

Table 1.10: Results of PGLS models describing the hypothesised causal relationships between brain size, body size, sociality and habitat temperature range under the combined model with social complexity data rounded up.

Outcome	Predictor	β	Std. Error	p-value	λ
Brain Mass	Body Mass	0.386	0.037	0	0.861
	Temperature Range	0.242	0.122	0.055	
	Sociality	0.083	0.031	0.012	
Sociality	Body Mass	0.468	0.186	0.016	0.905
Body Mass	Temperature Range	0.764	0.502	0.136	0.964

1.2 Adjusted Wheatsheaf Index Code

The following R code defines the new function *windex2* based on the *windex* function in the package of the same name. The new code calculates a Wheatsheaf index without correcting for phylogenetic relatedness between data points. Similarly, the second code updates the *test.windex* function to accept the output of the new *windex2* function.

```
windex2<-function (dat, tree, traits, focal = dat[, 2], SE = FALSE)
{
  if (class(tree) != "phylo")
    stop("Tree must be of class phylo")
  if (all(tree$edge.length == "NULL"))
    stop("Tree must contain branch lengths")
  if (is.ultrametric(tree) != TRUE)
    warning("Method is designed for ultrametric trees, your tree is
            not ultrametric so proceed with caution, if at all!")
  if (is.vector(dat[, traits]) == TRUE)
    if (is.numeric(dat[, traits]) != TRUE)
      stop("Trait data must be numeric")
  if (is.vector(dat[, traits]) != TRUE)
    for (i in 1:length(dat[, traits])) {
      if (is.numeric(dat[, traits[i]]) != TRUE)
        stop("Trait data must be numeric")
    }
  if (sort(unique(focal))[1] != 0)
    stop("Focals must be a binary string denoting non-focals as 0 and focals as 1")
  if (sort(unique(focal))[2] != 1)
    stop("Focals must be a binary string denoting non-focals as 0 and focals as 1")
  if (length(unique(focal)) != 2)
    stop("Focals must be a binary string denoting non-focals as 0 and focals as 1")
  rownames(dat) <- dat$species
  match <- match(tree$tip.label, rownames(dat))
  dat <- dat[, ][match, ]
  if (any(sort(rownames(dat)) != sort(tree$tip.label)))
    stop("Rownames of the data do not match the tip labels from the tree")
  if (SE == TRUE) {
    if (length(traits) == 1) {
      se <- sd(dat[, traits])/sqrt(length(dat[1, ]))
    }
    else {
      se <- sqrt(diag(var(dat[, traits]))/(length(dat[1,
                                                      ])))
    }
    data.w <- dat[, traits]/se
  }
  else data.w <- dat[, traits]
  dij <- as.matrix(dist(data.w, method = "euclidean", diag = T,
                        upper = T))
  Tree1 <- rescale(tree, model = "depth", 1)
  pij <- vcv(Tree1)
  dij. <- dij/(1 - log(pij + 0.01))
  da <- mean(dij.)
  df <- mean(dij.[which(focal == 1), which(focal == 1)])
  w.index <- da/df
  w.vec <- c()
  n <- length(dat[, 1])
  for (i in 1:n) {
    data <- data.w
    if (length(traits) == 1) {
      data[i] <- "NA"
    }
    else data[i, ] <- rep("NA", length(traits))
    options(warn = -1)
    dijJ <- as.matrix(dist(data, method = "euclidean", diag = T,
```

```
                            upper = T))
    options(warn = +1)
    Tree1 <- rescale(tree, model = "depth", 1)
    pij <- vcv(Tree1)
    dij.J <- dijJ/(1 - log(pij + 0.01))
    daJ <- mean(dij.J, na.rm = TRUE)
    dfJ <- mean(dij.J[which(focal == 1), which(focal == 1)],
                na.rm = TRUE)
    w <- daJ/dfJ
    w.vec[i] <- w
  }
  ave <- mean(w.vec)
  low <- quantile(w.vec, probs = 0.025, names = F)
  high <- quantile(w.vec, probs = 0.975, names = F)


  w.prime<-mean(dij)/mean(dij[which(focal == 1), which(focal == 1)])
  w.vec1 <- c()
  n <- length(dat[, 1])
  for (i in 1:n) {
    data <- data.w
    if (length(traits) == 1) {
      data[i] <- "NA"
    }
    else data[i, ] <- rep("NA", length(traits))
    options(warn = -1)
    dijJ <- as.matrix(dist(data, method = "euclidean", diag = T,
                           upper = T))
    options(warn = +1)
    daJ <- mean(dijJ, na.rm = TRUE)
    dfJ <- mean(dijJ[which(focal == 1), which(focal == 1)],
                na.rm = TRUE)
    w <- daJ/dfJ
    w.vec1[i] <- w
  }
  ave <- mean(w.vec1)
  low1 <- quantile(w.vec1, probs = 0.025, names = F)
  high1 <- quantile(w.vec1, probs = 0.975, names = F)
  w.diff<- w.index - w.prime


  return(list(`Wheatsheaf Index` = w.index, `Lower 95% CI` = low,
              `Upper 95% CI` = high, `Uncorrected W` = mouse,
              `Uncorrected Lower 95% CI` = low1,
              `Uncorrected Higher 95% CI` = high1,
              `Index Difference` = w.diff))
}
```

```
test.windex2<-function (dat, tree, traits, focal = dat[, 2], SE = TRUE, reps,
                        plot = TRUE, ...)
{
  w <- windex2(dat, tree, traits, focal, SE = SE)
  w.index <- w$"Wheatsheaf Index"
  l.ci <- w$"Lower 95% CI"
  u.ci <- w$"Upper 95% CI"


  w.index1<-w$"Uncorrected W"
  l.ci1<-w$"Uncorrected Lower 95% CI"
  u.ci1<-w$"Uncorrected Upper 95% CI"


  t.vec <- c()
  t.vec1<- c()
  pb <- txtProgressBar(min = 0, max = reps, style = 3)
  for (i in 1:reps) {
    info <- sprintf("%d%% done", round((i/reps) * 100))
    setTxtProgressBar(pb, i)
    X <- dat[, -1]
    new <- dat[sample(nrow(X), replace = TRUE), -1]
    newdat <- cbind(species = dat$species, new)
    w.rep <- windex2(newdat, tree, traits, focal)
    t.vec[i] <- w.rep$"Wheatsheaf Index"
```

```
    t.vec1[i] <- w.rep$"Uncorrected W"
  }
  p.val <- length(which(t.vec >= w.index))/reps
  if (plot == TRUE) {
    span <- max(c(t.vec, u.ci)) - min(c(t.vec, l.ci))
    leeway <- 0.1 * span
    hist(t.vec, xlab = "Wheatsheaf Index", main = "",
         xlim = c(min(c(t.vec,l.ci)) - leeway,
                  max(c(t.vec, u.ci)) + leeway), ...)
    abline(v = w.index)
    abline(v = l.ci, lty = 3)
    abline(v = u.ci, lty = 3)
    legend("top", horiz = TRUE, inset = c(0, -0.1), xpd = TRUE,
           bty = "n", c("Wheatsheaf index", "CI"), lty = c(1,
                                                           3))
  }


  p.val1 <- length(which(t.vec1 >= w.index1))/reps
  if (plot == TRUE) {
    span <- max(c(t.vec1, u.ci1)) - min(c(t.vec1, l.ci1))
    leeway <- 0.1 * span
    hist(t.vec1, xlab = "Uncorrected Wheatsheaf Index", main = "",
         xlim = c(min(c(t.vec1, l.ci1)) - leeway,
                  max(c(t.vec1, u.ci1)) + leeway), ...)
    abline(v = w.index1)
    abline(v = l.ci1, lty = 3)
    abline(v = u.ci1, lty = 3)
    legend("top", horiz = TRUE, inset = c(0, -0.1), xpd = TRUE,
           bty = "n", c("Wheatsheaf index", "CI"), lty = c(1,3))
  }
  close(pb)

  return(list(`P-value=` = p.val, `Uncorrected P-value` = p.val1))
}
```

1.3 Primate Data

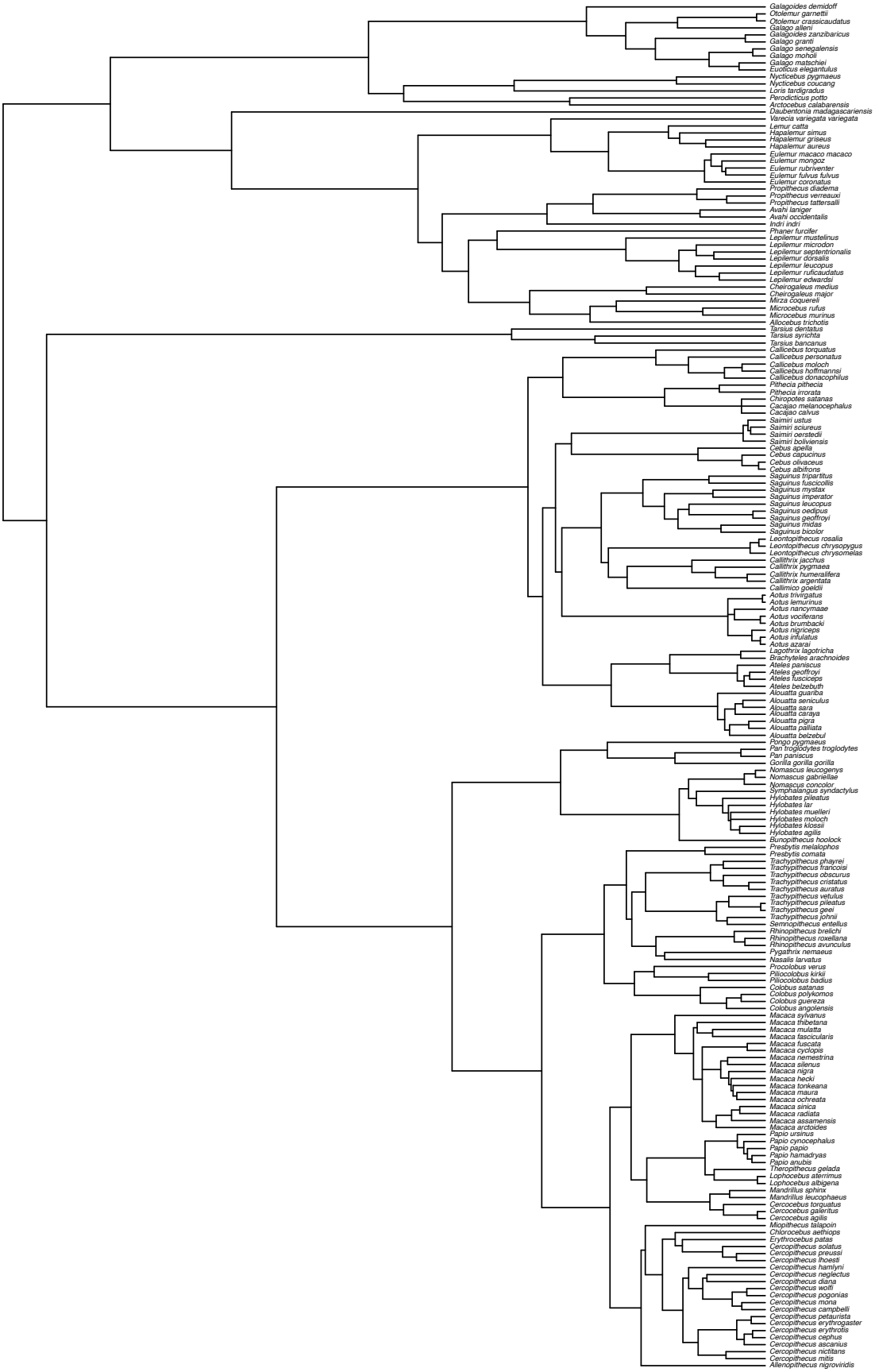

Figure 1.4: Consensus phylogeny of primates taken from the 10ktrees project (Arnold et al 2010).

Table 1.11: Binary classifications of four cognitively advanced behaviours taken from Reader et al. (2011). These behaviours are combined to classify species as either possessing advanced cognition or not. Research effort is indexed as the number of articles published in the Zoological Record for each species (Reader et al. 2011).

Species	Innovation	Social Transmission	Tool Use	Extractive Foraging	Advanced Cognition	Research Effort
Allenopithecus nigroviridis	0	0	0	0	0	6
Allocebus trichotis	0	0	0	0	0	6
Alouatta belzebul	0	0	0	0	0	15
Alouatta caraya	1	0	0	1	1	45
Alouatta guariba	1	0	0	0	1	37
Alouatta palliata	0	1	0	0	1	79
Alouatta pigra	0	0	0	0	0	25
Alouatta sara	0	0	0	0	0	4
Alouatta seniculus	1	0	1	0	1	82
Aotus azarai	0	0	0	0	0	22
Aotus brumbacki	0	0	0	0	0	0
Aotus infulatus	0	0	0	0	0	6
Aotus lemurinus	0	0	0	0	0	16
Aotus nancymaae	0	0	0	0	0	5
Aotus nigriceps	0	0	0	0	0	1
Aotus trivirgatus	0	0	0	0	0	58
Aotus vociferans	1	0	0	0	1	12

Species	Innovation	Social Transmission	Tool Use	Extractive Foraging	Advanced Cognition	Research Effort
Arctocebus calabarensis	0	0	0	0	0	1
Ateles belzebuth	0	0	0	0	0	12
Ateles fusciceps	0	0	0	0	0	4
Ateles geoffroyi	0	1	0	0	1	58
Ateles paniscus	0	0	0	0	0	30
Avahi laniger	0	0	0	0	0	10
Avahi occidentalis	0	0	0	0	0	6
Brachyteles arachnoides	0	0	0	0	0	57
Bunopithecus hoolock	0	0	0	0	0	24
Cacajao calvus	0	0	0	0	0	11
Cacajao melanocephalus	0	0	0	0	0	8
Callicebus donacophilus	0	0	0	0	0	1
Callicebus hoffmannsi	0	0	0	0	0	0
Callicebus moloch	0	0	0	0	0	18
Callicebus personatus	0	0	0	0	0	19
Callicebus torquatus	0	0	0	0	0	4
Callimico goeldii	1	0	0	1	1	43
Callithrix argentata	0	0	0	0	0	16
Callithrix humeralifera	0	0	0	0	0	4
Callithrix jacchus	1	1	0	1	1	161
Callithrix pygmaea	1	0	0	0	1	36
Cebus albifrons	0	1	1	1	1	13

Species	Innovation	Social Transmission	Tool Use	Extractive Foraging	Advanced Cognition	Research Effort
Cebus apella	1	1	1	1	1	249
Cebus capucinus	1	1	1	1	1	60
Cebus olivaceus	1	0	1	1	1	18
Cercocebus galeritus	0	0	0	1	1	19
Cercocebus torquatus	0	1	0	0	1	32
Cercopithecus ascanius	1	1	0	1	1	26
Cercopithecus campbelli	0	0	0	0	0	11
Cercopithecus cephus	0	0	0	0	0	8
Cercopithecus diana	0	1	0	0	1	28
Cercopithecus erythrogaster	0	0	0	0	0	3
Cercopithecus erythrotis	0	0	0	0	0	3
Cercopithecus hamlyni	0	0	0	0	0	4
Cercopithecus lhoesti	0	0	0	0	0	7
Cercopithecus mitis	1	0	0	1	1	56
Cercopithecus mona	0	0	0	0	0	8
Cercopithecus neglectus	0	0	0	0	0	17
Cercopithecus nictitans	0	0	0	0	0	7
Cercopithecus petaurista	0	0	0	0	0	5
Cercopithecus pogonias	0	0	0	0	0	8
Cercopithecus preussi	0	0	0	0	0	2
Cercopithecus solatus	0	0	0	0	0	6
Cercopithecus wolfi	0	0	0	0	0	7

Species	Innovation	Social Transmission	Tool Use	Extractive Foraging	Advanced Cognition	Research Effort
Cheirogaleus major	0	0	0	0	0	3
Cheirogaleus medius	0	0	0	0	0	13
Chiropotes satanas	1	0	0	1	1	21
Chlorocebus aethiops	1	1	1	1	1	91
Colobus angolensis	0	0	0	0	0	16
Colobus guereza	1	0	0	1	1	42
Colobus polykomos	0	0	0	0	0	17
Colobus satanas	0	0	0	0	0	10
Daubentonia madagascariensis	1	0	1	1	1	52
Erythrocebus patas	1	1	0	1	1	33
Eulemur coronatus	0	0	0	0	0	11
Eulemur fulvus	1	1	0	1	1	81
Eulemur macaco	1	0	1	1	1	32
Eulemur mongoz	1	0	0	1	1	13
Eulemur rubriventer	0	0	0	0	0	13
Euoticus elegantulus	0	0	0	0	0	1
Galago alleni	0	0	0	0	0	2
Galago granti	0	0	0	0	0	0
Galago matschiei	0	0	0	0	0	NA
Galago moholi	0	0	0	0	0	14
Galago senegalensis	0	0	0	0	0	20
Galagoides demidoff	0	0	0	0	0	5

Species	Innovation	Social Transmission	Tool Use	Extractive Foraging	Advanced Cognition	Research Effort
Galagoides zanzibaricus	0	0	0	0	0	0
Gorilla gorilla	1	1	1	1	1	517
Hapalemur aureus	0	0	0	0	0	5
Hapalemur griseus	0	0	0	0	0	40
Hapalemur simus	0	0	0	0	0	8
Hylobates agilis	0	0	0	0	0	16
Hylobates klossii	0	0	0	0	0	4
Hylobates lar	0	0	0	0	0	86
Hylobates moloch	0	0	0	0	0	16
Hylobates muelleri	0	0	0	0	0	5
Hylobates pileatus	1	0	0	0	1	16
Indri indri	0	0	0	0	0	8
Lagothrix lagotricha	0	0	0	0	0	34
Lemur catta	1	1	0	1	1	103
Leontopithecus chrysomelas	1	0	0	0	1	46
Leontopithecus chrysopygus	0	0	0	0	0	38
Leontopithecus rosalia	0	0	0	0	0	85
Lepilemur dorsalis	0	0	0	0	0	1
Lepilemur edwardsi	0	0	0	0	0	5
Lepilemur leucopus	0	0	0	0	0	2
Lepilemur microdon	0	0	0	0	0	1
Lepilemur mustelinus	0	0	0	0	0	5

Species	Innovation	Social Transmission	Tool Use	Extractive Foraging	Advanced Cognition	Research Effort
Lepilemur ruficaudatus	0	0	0	0	0	2
Lepilemur septentrionalis	0	0	0	0	0	0
Lophocebus albigena	0	0	0	0	0	34
Lophocebus aterrimus	0	0	0	0	0	6
Loris tardigradus	1	0	0	0	1	14
Macaca arctoides	1	1	1	1	1	48
Macaca assamensis	0	0	0	0	0	17
Macaca cyclopis	0	0	0	0	0	12
Macaca fascicularis	1	1	1	1	1	174
Macaca fuscata	1	1	1	1	1	253
Macaca maura	0	0	0	0	0	22
Macaca mulatta	1	1	1	1	1	296
Macaca nemestrina	1	1	1	1	1	51
Macaca nigra	0	0	1	1	1	27
Macaca ochreata	0	0	0	0	0	3
Macaca radiata	1	0	1	1	1	34
Macaca silenus	1	1	1	1	1	48
Macaca sinica	0	0	0	0	0	12
Macaca sylvanus	0	0	0	1	1	67
Macaca thibetana	0	1	0	0	1	42
Macaca tonkeana	1	1	1	1	1	26
Mandrillus leucophaeus	0	0	0	0	0	18

Species	Innovation	Social Transmission	Tool Use	Extractive Foraging	Advanced Cognition	Research Effort
Mandrillus sphinx	0	1	0	0	1	30
Microcebus murinus	0	0	0	0	0	66
Microcebus rufus	0	0	0	0	0	8
Miopithecus talapoin	0	0	0	0	0	4
Mirza coquereli	0	0	0	0	0	3
Nasalis larvatus	0	0	0	0	0	17
Nomascus concolor	0	0	0	0	0	21
Nomascus gabriellae	1	0	0	0	1	4
Nomascus leucogenys	0	0	0	0	0	8
Nycticebus coucang	0	0	0	0	0	37
Nycticebus pygmaeus	0	0	0	0	0	19
Otolemur crassicaudatus	1	1	0	1	1	36
Otolemur garnettii	1	1	0	0	1	12
Pan paniscus	1	1	1	1	1	225
Pan troglodytes	1	1	1	1	1	755
Papio anubis	1	1	1	1	1	43
Papio cynocephalus	0	1	0	0	1	114
Papio hamadryas	1	1	1	1	1	78
Papio papio	1	1	1	1	1	8
Papio ursinus	1	1	1	1	1	22
Perodicticus potto	0	0	0	0	0	10
Phaner furcifer	0	0	0	0	0	1

Species	Innovation	Social Transmission	Tool Use	Extractive Foraging	Advanced Cognition	Research Effort
Piliocolobus badius	0	0	0	0	0	52
Piliocolobus kirkii	1	1	0	0	1	7
Pithecia irrorata	0	0	0	0	0	7
Pithecia pithecia	0	0	0	0	0	28
Pongo pygmaeus	1	1	1	1	1	321
Presbytis comata	0	0	0	0	0	11
Presbytis melalophos	0	0	0	0	0	6
Procolobus verus	0	0	0	0	0	3
Propithecus diadema	0	0	0	0	0	28
Propithecus tattersalli	0	0	0	0	0	9
Propithecus verreauxi	0	1	0	0	1	41
Pygathrix nemaeus	0	0	0	0	0	25
Rhinopithecus avunculus	0	0	0	0	0	11
Rhinopithecus brelichi	0	0	0	0	0	16
Rhinopithecus roxellana	1	0	0	1	1	36
Saguinus bicolor	0	0	0	0	0	9
Saguinus fuscicollis	1	1	1	1	1	81
Saguinus imperator	0	0	0	0	0	16
Saguinus leucopus	0	0	0	0	0	3
Saguinus midas	0	0	0	0	0	17
Saguinus mystax	1	0	0	0	1	46
Saguinus oedipus	0	0	0	0	0	153

Species	Innovation	Social Transmission	Tool Use	Extractive Foraging	Advanced Cognition	Research Effort
Saguinus tripartitus	0	0	0	0	0	5
Saimiri boliviensis	0	0	0	0	0	36
Saimiri oerstedii	0	1	0	0	1	4
Saimiri sciureus	1	1	0	1	1	89
Saimiri ustus	0	0	0	0	0	4
Semnopithecus entellus	1	1	0	1	1	98
Symphalangus syndactylus	0	0	0	0	0	40
Tarsius bancanus	0	0	0	0	0	8
Tarsius dentatus	0	0	0	0	0	2
Tarsius syrichta	0	0	0	0	0	10
Theropithecus gelada	0	0	0	0	0	34
Trachypithecus auratus	0	0	0	0	0	2
Trachypithecus cristatus	0	0	0	0	0	8
Trachypithecus francoisi	0	0	0	0	0	45
Trachypithecus geei	0	0	0	0	0	7
Trachypithecus johnii	0	1	0	0	1	9
Trachypithecus obscurus	0	0	0	0	0	6
Trachypithecus phayrei	0	0	0	0	0	16
Trachypithecus pileatus	0	0	0	0	0	5
Trachypithecus vetulus	0	0	0	0	0	2
Varecia variegata	0	0	0	0	0	57

Table 1.12: Data on social group size, home range, longevity, diet breadth, (0:Solitary, 1:Social), terrestriality (0:Arboreal, 1:Terrestrial), habitat openness (0:Open, 1:Closed) and activity pattern (0:Nocturnal, 1:Diurnal) in primates.

Species	Social Group Size	Home Range	Longevity	Diet Breadth	Sociality	Terrestriality	Habitat Openness	Activity Pattern
Allenopithecus nigroviridis	40.0		28.00		1	1	0	1
Allocebus trichotis	1.0			4	0	0	0	0
Alouatta belzebul	7.4				1	0	0	1
Alouatta caraya	8.9	5.90		3	1	0	0	1
Alouatta guariba	6.8	5.40		4	1	0	0	1
Alouatta palliata	13.7	43.30	20.00	2	1	0	0	1
Alouatta pigra	5.4	73.20		2	1	0	0	1
Alouatta sara								
Alouatta seniculus	8.0	12.10	25.00	6	1	0	0	1
Aotus azarai	4.1			2	1	0	0	0
Aotus brumbacki								0
Aotus infulatus								0
Aotus lemurinus				4				0
Aotus nancymaae	4.0			2	1			0
Aotus nigriceps	3.3			2	1			0
Aotus trivirgatus	3.8	7.10	20.00	3	1	0	0	0
Aotus vociferans	3.3			2	1			0
Arctocebus calabarensis	1.0		11.25	3	0	0	0	0

Species	Social Group Size	Home Range	Longevity	Diet Breadth	Sociality	Terrestriality	Habitat Openness	Activity Pattern
Ateles belzebuth	22.0	441.00	20.00	2	1	0	0	1
Ateles fusciceps			24.00	2		0	0	1
Ateles geoffroyi	42.0	133.10	27.30	2	1	0	0	1
Ateles paniscus	38.5	206.00	33.00	6	1	0	0	1
Avahi laniger	2.5	1.90		3	1	0	0	0
Avahi occidentalis	2.5			1	1			0
Brachyteles arachnoides	19.2	294.85	30.00	5	1	0	0	1
Bunopithecus hoolock	3.6	24.20	42.00	5	1	0	0	1
Cacajao calvus	30.0	550.00	20.10	4	1	0	0	1
Cacajao melanocephalus	30.0			3	1	0	0	1
Callicebus donacophilus								1
Callicebus hoffmannsi								
Callicebus moloch	3.3	5.70	11.00	3	1	0	0	1
Callicebus personatus	3.7	4.70		4	1	0	0	1
Callicebus torquatus	4.0	18.10		4	1	0	0	1
Callimico goeldii	7.7	42.50	13.60	2	1	0	0	1
Callithrix argentata	9.5	5.00		4	1	0	0	1
Callithrix humeralifera	11.5	20.60	12.50	4	1	0	0	1
Callithrix jacchus	8.4	12.50	11.85	5	1	0	0	1
Callithrix pygmaea	5.7	0.70	11.69	3	1	0	0	1
Cebus albifrons	16.8	137.75	44.00	5	1	0	0	1
Cebus apella	11.1	344.00	44.00	6	1	0	0	1

Species	Social Group Size	Home Range	Longevity	Diet Breadth	Sociality	Terrestriality	Habitat Openness	Activity Pattern
Cebus capucinus	21.0	86.30	46.90	4	1	0	0	1
Cebus olivaceus	17.1	257.00		4	1	0	0	1
Cercocebus agilis								
Cercocebus galeritus	18.3	117.75	19.00	2	1	1	0	1
Cercocebus torquatus	26.8	247.00	27.00	1	1	1	0	1
Cercopithecus ascanius	26.3	31.20	22.50	4	1	0	0	1
Cercopithecus campbelli	14.0	21.50		3	1	1	0	1
Cercopithecus cephus	11.0	34.00	22.00	3	1	0	0	1
Cercopithecus diana	23.0	100.70	34.80	3	1	0	0	1
Cercopithecus erythrogaster				2		0	0	1
Cercopithecus erythrotis				2		0	0	1
Cercopithecus hamlyni						0	0	1
Cercopithecus lhoesti	17.4	850.00		3	1	1	0	1
Cercopithecus mitis	16.3	83.80	20.00	4	1	0	0	1
Cercopithecus mona		3.00	22.00			0	0	1
Cercopithecus neglectus	5.0	7.40	22.00	3	1	1	0	1
Cercopithecus nictitans	16.0	120.75		4	1	0	0	1
Cercopithecus petaurista	14.0	41.00			1	0	0	1
Cercopithecus pogonias	15.0	103.00	20.00	3	1	0	0	1
Cercopithecus preussi	5.0			4	1	1	0	1
Cercopithecus solatus	10.0				1	1	0	1
Cercopithecus wolfi						0	0	1

Species	Social Group Size	Home Range	Longevity	Diet Breadth	Sociality	Terrestriality	Habitat Openness	Activity Pattern
Cheirogaleus major	1.0		8.80	5	0	0	0	0
Cheirogaleus medius	1.0		9.00	5	0	0	0	0
Chiropotes satanas	9.7	239.00		3	1	0	0	1
Chlorocebus aethiops	28.9	70.40	27.50		1	1	1	1
Colobus angolensis	10.9			1	1	0	0	1
Colobus guereza	8.3	12.60	22.27	2	1	0	0	1
Colobus polykomos	10.2	36.00	28.25	2	1	0	0	1
Colobus satanas	15.5	71.80		3	1	0	0	1
Daubentonia madagascariensis	1.0	35.60	22.80	6	0	0	0	0
Erythrocebus patas	28.0	2997.50	21.59	4	1	1	1	1
Eulemur coronatus	8.4			4	1	0	0	1
Eulemur fulvus fulvus	9.2	48.60	30.44	3	1	0	0	1
Eulemur macaco macaco	8.4	5.30	27.09	4	1	0	0	1
Eulemur mongoz	3.5		25.33	4	1	0	0	0
Eulemur rubriventer	3.2			4	1	0	0	1
Euoticus elegantulus	1.0			4	0	0	0	0
Galago alleni	1.0	12.00	12.00	2	0	0	0	0
Galago granti						0	0	0
Galago matschiei	1.0				0	0	0	0
Galago moholi	1.0	8.10	16.50	2	0	0	0	0
Galago senegalensis	1.0		16.25	3	0	0	0	0
Galagoides demidoff	1.0	0.90	13.50	4	0	0	0	0

Species	Social Group Size	Home Range	Longevity	Diet Breadth	Sociality	Terrestriality	Habitat Openness	Activity Pattern
Galagoides zanzibaricus	1.0	2.20		4	0	0	0	0
Gorilla gorilla gorilla	7.0	2542.25	50.00	3	1	1	0	1
Hapalemur aureus	3.0			2	1	0	0	1
Hapalemur griseus	2.6	11.30	12.05	2	1	0	0	0
Hapalemur simus	8.0				1	0	0	1
Hylobates agilis	4.4	27.00		4	1	0	0	1
Hylobates klossii	3.6	21.50		3	1	0	0	1
Hylobates lar	3.9	34.20	31.50	4	1	0	0	1
Hylobates moloch	3.3	17.40	35.00	4	1	0	0	1
Hylobates muelleri	3.4		47.00	4	1	0	0	1
Hylobates pileatus	3.5	36.00	39.00	5	1	0	0	1
Indri indri	3.1	22.50		4	1	0	0	1
Lagothrix lagotricha	16.7	544.90	25.91	4	1	0	0	1
Lemur catta	15.3	14.40	27.10	4	1	1	0	1
Leontopithecus chrysomelas	6.7				1	0	0	1
Leontopithecus chrysopygus	3.6			4	1	0	0	1
Leontopithecus rosalia	7.2		14.19	3	1	0	0	1
Lepilemur dorsalis	1.0			3	0			0
Lepilemur edwardsi	1.0			5	0			0
Lepilemur leucopus	1.0			2	0			0
Lepilemur microdon	1.0			4	0			0
Lepilemur mustelinus	1.0			3	0	0	0	0

Species	Social Group Size	Home Range	Longevity	Diet Breadth	Sociality	Terrestriality	Habitat Openness	Activity Pattern
Lepilemur ruficaudatus	1.0			2	0			0
Lepilemur septentrionalis	1.0			3	0			0
Lophocebus albigena	16.6	270.85	32.70	3	1	0	0	1
Lophocebus aterrimus		59.00				0	0	1
Loris tardigradus	1.0		12.00	4	0	0	0	0
Macaca arctoides			30.00	1		1	0	1
Macaca assamensis	21.0				1	0	0	1
Macaca cyclopis	20.2	19.50			1	1	0	1
Macaca fascicularis	27.0	69.30	37.09	3	1	0	0	1
Macaca fuscata	45.0	177.05	33.00	5	1	1	0	1
Macaca hecki								
Macaca maura		25.00				0	0	1
Macaca mulatta	36.0	396.10	29.00	1	1	1	0	1
Macaca nemestrina	18.3	355.10	26.30	2	1	0	0	1
Macaca nigra	35.0	260.00	18.00	1	1	1	0	1
Macaca ochreata						0	0	1
Macaca radiata	24.9	188.00	30.00		1	0	0	1
Macaca silenus	26.5	50.70	38.00	4	1	0	0	1
Macaca sinica	21.6	51.80	30.00	2	1	0	0	1
Macaca sylvanus	18.3	618.40	22.00	6	1	1	0	1
Macaca thibetana	21.0	300.00	20.00		1	1	0	1
Macaca tonkeana						1	0	1

Species	Social Group Size	Home Range	Longevity	Diet Breadth	Sociality	Terrestriality	Habitat Openness	Activity Pattern
Mandrillus leucophaeus	17.0		28.80	3	1	1	0	1
Mandrillus sphinx	251.2	3080.00	36.22	4	1	1	0	1
Microcebus murinus	1.0		15.46	5	0	0	0	0
Microcebus rufus	1.0			5	0	0	0	0
Miopithecus talapoin	115.0	121.80	27.68	3	1	0	0	1
Mirza coquereli	1.0		15.25	4	0	0	0	0
Nasalis larvatus	10.5	261.00	13.50	4	1	0	0	1
Nomascus concolor	4.0	87.50	36.00	5	1	0	0	1
Nomascus gabriellae								
Nomascus leucogenys								1
Nycticebus coucang	1.0		15.25	6	0	0	0	0
Nycticebus pygmaeus	1.0		20.00		0	0	0	0
Otolemur crassicaudatus	1.0	7.00	15.00	5	0	0	0	0
Otolemur garnettii	1.0	12.00	17.00	3	0	0	0	0
Pan paniscus	85.0	3477.50	40.00	6	1	1	0	1
Pan troglodytes troglodytes	60.0	1788.40	53.00	6	1	1	0	1
Papio anubis	40.0	1841.55	45.00		1	1	1	1
Papio cynocephalus	55.4	4562.00	40.00	2	1	1	1	1
Papio hamadryas	7.3	2800.00	35.60	2	1	1	1	1
Papio papio		1300.00	40.00			1	1	1
Papio ursinus	57.1	1122.05	45.00	2	1	1	1	1
Perodicticus potto	1.0	11.80	22.32	4	0	0	0	0

Species	Social Group Size	Home Range	Longevity	Diet Breadth	Sociality	Terrestriality	Habitat Openness	Activity Pattern
Phaner furcifer	2.5			3	1	0	0	0
Piliocolobus badius	34.0	57.50		3	1	0	0	1
Piliocolobus kirkii				4		0	0	1
Pithecia irrorata	4.4				1			1
Pithecia pithecia	2.7	7.00	13.78	2	1	0	0	1
Pongo pygmaeus	1.0	169.80	57.31	5	0	0	0	1
Presbytis comata	6.5			3	1	0	0	1
Presbytis melalophos	11.6	25.25		1	1	0	0	1
Procolobus verus	6.3	26.50		1	1	0	0	1
Propithecus diadema	5.1		20.00	3	1	0	0	1
Propithecus tattersalli	4.1			4	1	0	0	1
Propithecus verreauxi	6.0	5.30	18.18	3	1	0	0	1
Pygathrix nemaeus	9.3		10.25	2	1	0	0	1
Rhinopithecus avunculus	25.0				1	0	0	1
Rhinopithecus brelichi	6.1			2	1	0	0	1
Rhinopithecus roxellana		3145.00		2		1	0	1
Saguinus bicolor	6.7	12.00		4	1	0	0	1
Saguinus fuscicollis	5.1	34.30		5	1	0	0	1
Saguinus geoffroyi		29.00		4		0		
Saguinus imperator	6.0	52.50	17.00	2	1	0	0	1
Saguinus leucopus				5		0	0	1
Saguinus midas	6.4		13.28	4	1	0	0	1

Species	Social Group Size	Home Range	Longevity	Diet Breadth	Sociality	Terrestriality	Habitat Openness	Activity Pattern
Saguinus mystax	5.5	32.30	20.00	5	1	0	0	1
Saguinus oedipus	7.2	15.70	13.50	4	1	0	0	1
Saguinus tripartitus			6.00			0	0	1
Saimiri boliviensis	60.0				1			1
Saimiri oerstedii	50.0	62.60		2	1	0	0	1
Saimiri sciureus	35.0	149.15	21.00	3	1	0	0	1
Saimiri ustus								1
Semnopithecus entellus	25.0	185.95	25.00	2	1	1	0	1
Symphalangus syndactylus	3.6	26.50	35.00	4	1	0	0	1
Tarsius bancanus	1.0	3.10	12.00	3	0	0	0	0
Tarsius dentatus	1.0				0			0
Tarsius syrichta	1.0		13.50	1	0	0	0	0
Theropithecus gelada	10.0	212.00	19.27	2	1	1	1	1
Trachypithecus auratus	11.0				1	0	0	1
Trachypithecus cristatus	22.8	20.00			1	0	0	1
Trachypithecus francoisi		157.00		1		0	0	1
Trachypithecus geei	12.5	375.00			1	0	0	1
Trachypithecus johnii	14.8	161.60		1	1	0	0	1
Trachypithecus obscurus	17.0	34.30		1	1	0	0	1
Trachypithecus phayrei	12.9	75.00			1	0	0	1
Trachypithecus pileatus	8.5	42.50			1	0	0	1
Trachypithecus vetulus	8.8	4.40		2	1			

Species	Social Group Size	Home Range	Longevity	Diet Breadth	Sociality	Terrestriality	Habitat Openness	Activity Pattern
Varecia variegata variegata	5.3	110.20	13.00	4	1	0	0	1

1.4 Cetacean Data

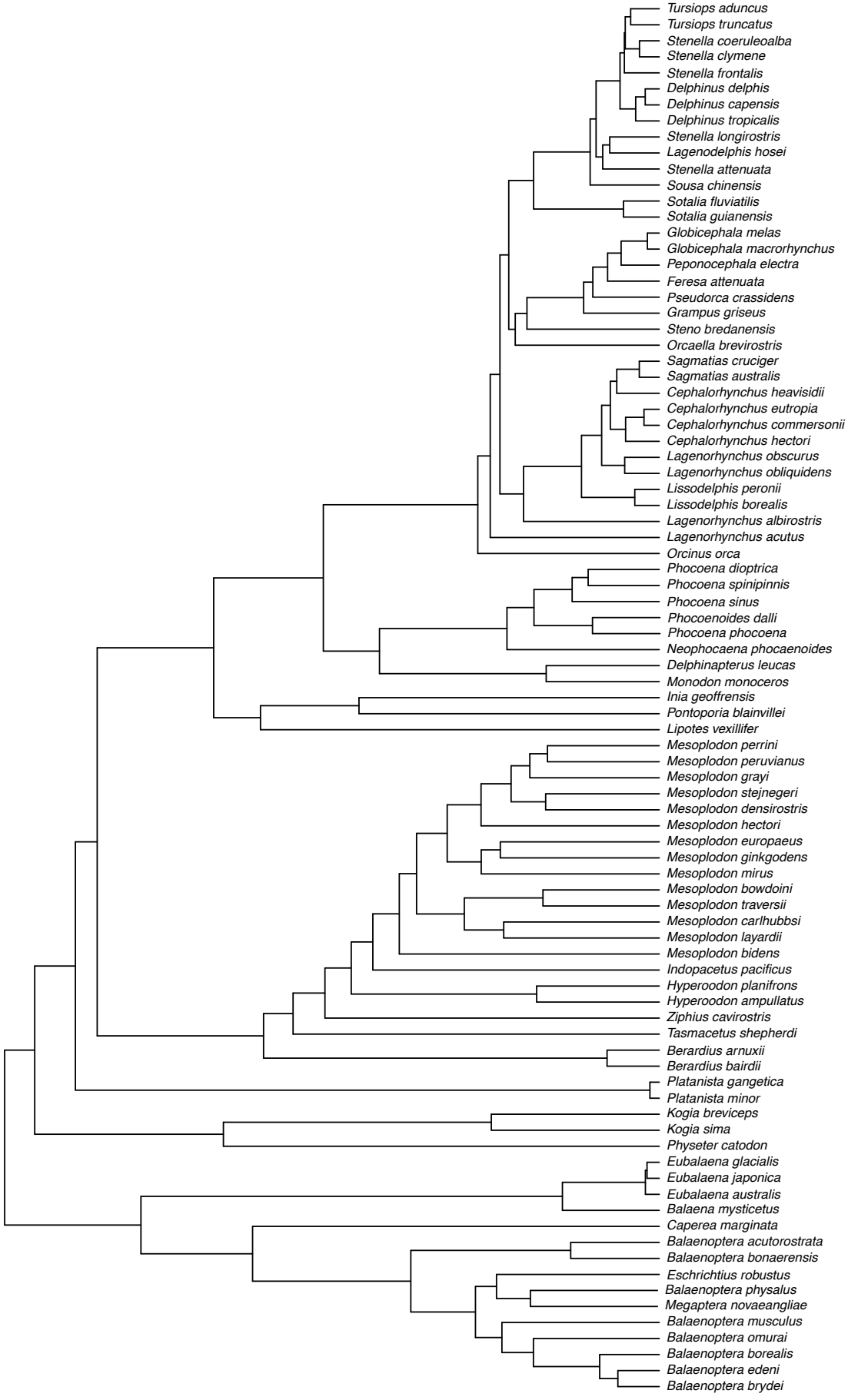

Figure 1.5: Phylogeny of cetaceans (McGowen et al 2009).

Table 1.13: Data on brain size, body size, sociality and habitat temperature for cetaceans.

Species	Body Mass	Brain Mass	Sociality	Minimum Habitat Temperature	Maximum Habitat Temperature	Temperature Range
Balaena mysticetus	90999999.9	2738.00	0.0	-1.77	9.27	11.04
Balaenoptera acutorostrata				-1.85	30.28	32.13
Balaenoptera bonaerensis			0.0	-1.87	29.17	31.04
Balaenoptera borealis	20000000.0	4900.00	0.0	-1.82	30.28	32.10
Balaenoptera edeni			0.0	6.16	30.33	24.17
Balaenoptera musculus	50904000.0	3636.00	0.0	-1.87	30.29	32.16
Balaenoptera physalus	33221430.0	7111.43	0.0	-1.85	29.78	31.63
Berardius arnuxii				-1.87	25.27	27.14
Berardius bairdii				0.28	25.98	25.70
Caperea marginata			0.0	-0.33	25.02	25.36
Cephalorhynchus commersonii	48000.0	725.00	1.0	-0.73	13.37	14.10
Cephalorhynchus eutropia			1.0	7.00	14.89	7.89
Cephalorhynchus heavisidii	71000.0	763.00	1.0	12.78	21.75	8.97
Cephalorhynchus hectori			1.0	9.89	18.00	8.11
Delphinapterus leucas	636000.0	2083.00	1.5	-1.68	11.02	12.70
Delphinus capensis				11.39	29.73	18.34
Delphinus delphis	60170.0	815.00	1.5	0.00	30.21	30.21
Eschrichtius robustus	30000000.0	4316.67	0.0	-1.05	27.35	28.40
Eubalaena australis				-1.54	27.99	29.53

Species	Body Mass	Brain Mass	Sociality	Minimum Habitat Temperature	Maximum Habitat Temperature	Temperature Range
Eubalaena glacialis			0.0	-0.86	27.28	28.14
Eubalaena japonica				0.28	25.98	25.70
Feresa attenuata				12.31	30.33	18.02
Globicephala macrorhynchus	386000.0	2466.00	3.0	0.00	30.33	30.33
Globicephala melas	1061000.0	2673.00	3.0	-1.42	30.21	31.63
Grampus griseus	400000.0	2551.00	1.5	0.35	30.29	29.94
Hyperoodon ampullatus			2.0	-1.24	25.41	26.65
Hyperoodon planifrons				-1.87	26.53	28.39
Indopacetus pacificus				13.89	30.33	16.44
Inia geoffrensis	92003.5	633.64	0.5	22.00	32.00	10.00
Kogia breviceps	334000.0	1019.00		0.00	30.29	30.29
Kogia sima	168500.0	622.00	1.0	6.41	30.28	23.87
Lagenodelphis hosei			2.0	12.78	30.28	17.50
Lagenorhynchus acutus	244605.0	1103.17	1.0	-0.86	16.61	17.48
Lagenorhynchus albirostris	67500.0	1126.00	1.0	-1.36	17.96	19.32
Lagenorhynchus australis				0.22	16.33	16.11
Lagenorhynchus cruciger				-1.49	20.83	22.33
Lagenorhynchus obliquidens	91050.0	1147.75	1.0	0.00	25.98	25.98
Lagenorhynchus obscurus	58473.1	886.10	1.5	2.95	26.52	23.57
Lipotes vexillifer	180000.0	558.00	0.5	9.00	17.00	8.00
Lissodelphis borealis	73000.0	1162.00		0.00	23.82	23.82
Lissodelphis peronii				-0.88	26.69	27.57

Species	Body Mass	Brain Mass	Sociality	Minimum Habitat Temperature	Maximum Habitat Temperature	Temperature Range
Megaptera novaeangliae	39311330.0	6439.00	0.0	-1.87	30.33	32.20
Mesoplodon bidens				1.66	23.45	21.79
Mesoplodon bowdoini				-0.52	22.96	23.48
Mesoplodon carlhubbsi				3.93	23.92	19.99
Mesoplodon densirostris	770500.0	1424.50	0.0	0.00	30.33	30.33
Mesoplodon europaeus	732500.0	2149.00		4.13	28.42	24.29
Mesoplodon ginkgodens				9.90	30.25	20.35
Mesoplodon grayi				-1.72	26.78	28.50
Mesoplodon hectori				-0.60	23.93	24.53
Mesoplodon layardii				-1.31	25.04	26.35
Mesoplodon mirus	929500.0	2355.00		3.54	26.77	23.23
Mesoplodon perrini				12.92	16.94	4.02
Mesoplodon peruvianus				14.33	29.63	15.30
Mesoplodon stejnegeri				0.00	25.88	25.88
Mesoplodon traversii				5.54	22.16	16.61
Monodon monoceros	1578330.0	2993.70	3.0	-1.78	7.75	9.52
Neophocaena phocaenoides	32400.0	468.00	1.0	20.98	29.69	8.71
Orcaella brevirostris			0.0	26.95	30.33	3.38
Orcinus orca	2049000.0	5617.00	3.0	-1.87	30.02	31.89
Peponocephala electra			3.0	12.78	30.29	17.51
Phocoena dioptrica				-1.29	23.68	24.97
Phocoena phocoena	61100.0	500.00	1.0	-1.38	25.88	27.26

Species	Body Mass	Brain Mass	Sociality	Minimum Habitat Temperature	Maximum Habitat Temperature	Temperature Range
Phocoena sinus			1.0	21.68	23.54	1.86
Phocoena spinipinnis	68041.9	597.00	1.0	5.88	21.63	15.75
Phocoenoides dalli	112000.0	867.00	1.0	0.78	22.08	21.30
Physeter catodon	37416650.0	8183.10	3.0	-1.79	30.28	32.07
Platanista gangetica	59630.0	290.50	0.0	8.00	33.00	25.00
Platanista minor	18300.0	164.00	0.0	8.00	33.00	25.00
Pontoporia blainvillei	34900.0	221.00	1.0	12.86	25.87	13.01
Pseudorca crassidens	579196.4	3512.00	3.0	-0.38	30.25	30.63
Sotalia fluviatilis	42240.0	688.00	2.0	20.00	32.00	12.00
Sousa chinensis			1.5	16.03	30.33	14.30
Sousa teuszii				18.18	28.26	10.08
Stenella attenuata			1.5	6.93	30.29	23.36
Stenella clymene	86000.0	666.00	1.0	12.56	28.70	16.14
Stenella coeruleoalba	129600.0	939.40	1.5	3.70	29.69	25.99
Stenella frontalis			1.5	4.13	28.70	24.57
Stenella longirostris	66200.0	660.00	1.5	10.71	30.29	19.58
Steno bredanensis	123830.9	1541.90	2.0	0.00	30.29	30.29
Tasmacetus shepherdi				0.36	23.13	22.77
Tursiops aduncus				14.90	30.29	15.39
Tursiops truncatus	214580.0	1676.48	1.5	4.20	30.33	26.13
Ziphius cavirostris	2273000.0	2004.00	0.0	2.78	29.63	26.85

1.5 Bird Data

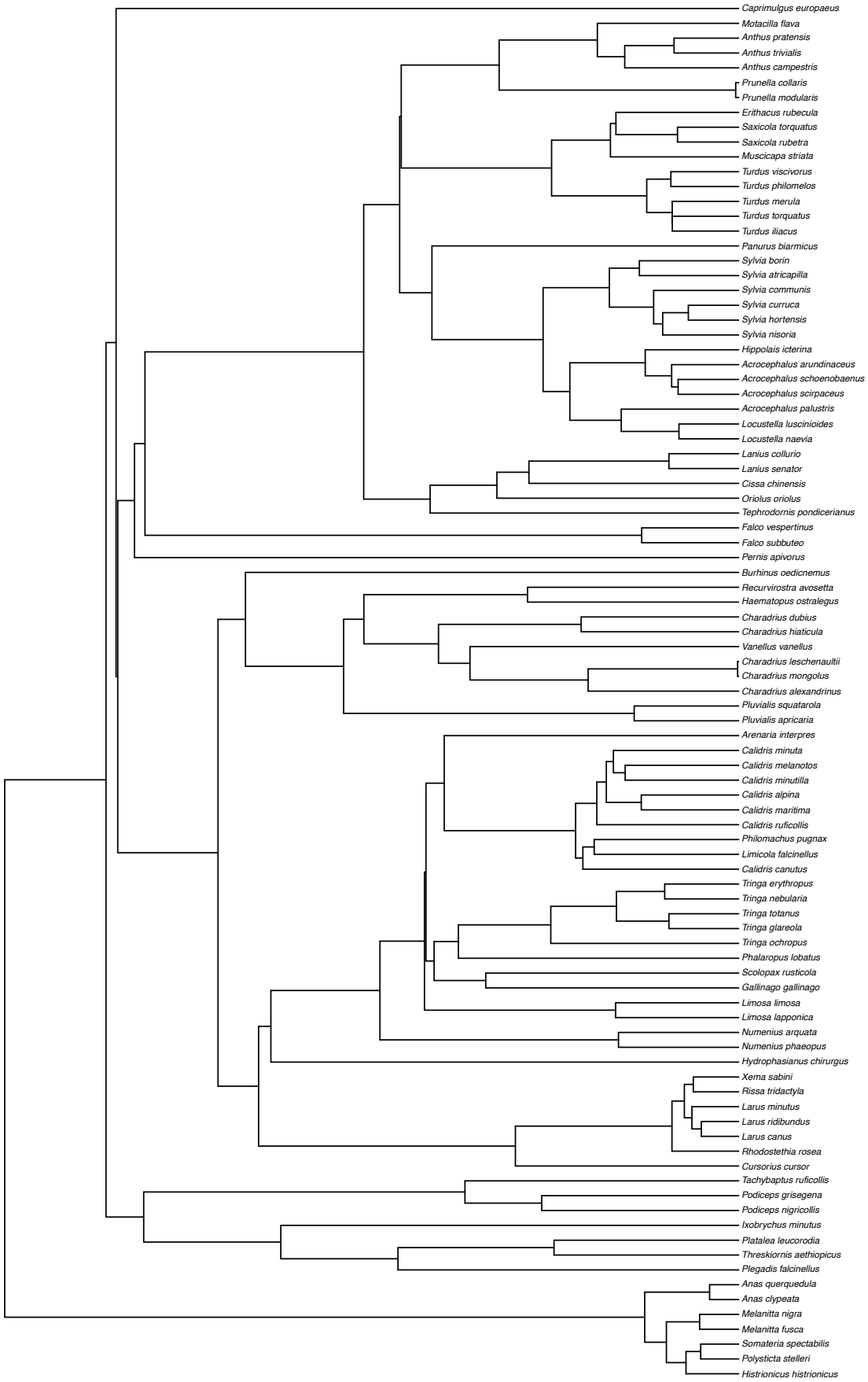

Figure 1.6: Example phylogeny of potential cuckoo hosts from a block of 1000 avian trees (Jetz et al 2012).

Table 1.14: Phenotypic data on brain size, body mass, nest type, diet, vocal mimicry, sociality, migration and whether or not a species is parasitised in species with breeding ranges overlapping that of the European cuckoo (*Cuculus canorus).*

Species	Body Mass	Vocal Mimicry	Diet	Sociality	Migration	Nest Type	Parasitised	Brain Volume
Accipiter brevipes	190.00	0	vertfishscav	1	1	open	0	3.19
Accipiter gentilis	936.32	0	vertfishscav	0	1	open	0	7.88
Accipiter nisus	230.29	0	vertfishscav	0	1	open	0	2.81
Aceros undulatus	2232.50	0	fruit		0		0	18.25
Acridotheres tristis	115.60	1	omnivore	1	0	cavity	1	2.48
Acrocephalus arundinaceus	25.90	0	invertebrate		1	open	1	0.91
Acrocephalus melanopogon	11.27	0	invertebrate		1		0	0.40
Acrocephalus palustris	11.85	1	invertebrate		1	open	0	0.44
Acrocephalus schoenobaenus	11.35	1	invertebrate		1	open	0	0.45
Acrocephalus scirpaceus	12.70	1	invertebrate	0	1	open	1	0.51
Acrocephalus stentoreus	26.90	1	invertebrate		1		0	0.84
Actitis hypoleucos	49.35		invertebrate	0	1		0	0.80
Aegithalos caudatus	7.93	0	invertebrate	1	0	closed	0	0.45
Aegithalos concinnus	6.10	0	invertebrate	1	0		0	0.37
Aegithina tiphia	12.30	0	invertebrate	0	0		1	0.67
Aegolius funereus	91.20	0	vertfishscav		0	cavity	0	4.02
Aegypius monachus	9312.50	0	vertfishscav	1	1	open	0	26.35
Aethia cristatella	84.60		invertebrate	1			0	1.48

Species	Body Mass	Vocal Mimicry	Diet	Sociality	Migration	Nest Type	Parasitised	Brain Volume
Aethia pusilla	84.60		invertebrate	1	1		0	1.48
Aethopyga nipalensis	6.00	0	nectar	1	1		1	0.33
Alauda arvensis	37.57	1	seed	1	1	open	0	0.96
Alca torda	720.67		vertfishscav	1	1	open	0	5.38
Alcedo atthis	34.67	0	vertfishscav		1		0	0.74
Alectoris barbara	500.00	0	vegetation		0	open	0	2.70
Alectoris chukar	536.33	0	seed	1	0	open	0	2.49
Alectoris graeca	637.50	0	vegetation		0	open	0	2.03
Alectoris rufa	477.50	0	vegetation		0	open	0	1.89
Alophoixus pallidus	46.00	0	fruit	1	0		0	1.24
Alopochen aegyptiaca	1938.00	0	vegetation	1	0	open	0	6.93
Amandava amandava	9.75	0	seed	1	0		0	0.38
Amaurornis phoenicurus	478.40	0	invertebrate		1		0	2.34
Anas acuta	894.75	0	omnivore	1	1	open	1	4.72
Anas clypeata	577.95	0	invertebrate	1	1	open	1	3.42
Anas crecca	322.50	0	vegetation	1	1	open	0	2.55
Anas penelope	735.75	0	vegetation	1	1	open	0	3.86
Anas querquedula	326.00	0	invertebrate		1	open	0	2.70
Anhinga melanogaster	1608.30	0	vertfishscav		0		0	4.56
Anous stolidus	172.50		vertfishscav		1	open	0	2.23
Anser albifrons	2900.25	0	vegetation	1	1	open	0	9.09
Anser erythropus	1797.50	0	vegetation		1	open	0	6.47

Species	Body Mass	Vocal Mimicry	Diet	Sociality	Migration	Nest Type	Parasitised	Brain Volume
Anser fabalis	2709.00	0	vegetation	1	1	open	0	10.65
Anthus campestris	22.95	0	invertebrate		1	open	0	0.48
Anthus pratensis	17.88	0	invertebrate	1	1	open	0	0.49
Anthus spinoletta	20.70	0	invertebrate	1	1	closed	0	0.56
Anthus trivialis	20.90	0	invertebrate	1	1	open	1	0.60
Apus apus	38.65	0	invertebrate	1	1	cavity	0	0.66
Apus pallidus	41.90	0	invertebrate	1	1	cave	0	0.72
Aquila chrysaetos	4484.38	0	vertfishscav	1	1	open	0	17.19
Aquila clanga	1916.80	0	vertfishscav		1	open	0	11.39
Aquila fasciatus	2000.00	0	vertfishscav	1	0	open	0	10.50
Aquila heliaca	3262.00	0	vertfishscav	1	1	open	0	14.96
Aquila pomarina	1475.40	0	vertfishscav		1	open	0	10.91
Aquila rapax	2250.00	0	vertfishscav		0	open	0	13.31
Arachnothera longirostra	11.70	0	nectar	1	0	closed	1	0.52
Ardea cinerea	1565.27	0	vertfishscav	0	1	open	0	8.45
Arenaria interpres	101.50		invertebrate	1	1	open	0	1.34
Asio capensis	310.00	0	vertfishscav		1	open	0	5.98
Asio flammeus	329.84	0	vertfishscav	0	0	open	0	5.30
Asio otus	249.67	0	vertfishscav	0	1	open	0	5.32
Athene noctua	164.50	0	vertfishscav	0	0	cavity	0	3.70
Bombycilla garrulus	55.78	0	fruit	1	1	open	0	1.13
Bonasa bonasia	36.50	0	vegetation	1	0	open	0	1.82

Species	Body Mass	Vocal Mimicry	Diet	Sociality	Migration	Nest Type	Parasitised	Brain Volume
Botaurus stellaris	1680.75	0	vertfishscav	0	1	open	0	5.89
Brachypteryx montana	18.00	0	invertebrate		0		1	0.83
Bubo bubo	2343.00	0	vertfishscav	0	0	open	0	17.09
Bubo scandiaca	1894.00	0	vertfishscav	0	1	open	0	15.87
Bucanetes githagineus	18.15	0	seed	1	1		0	0.64
Buceros bicornis	2798.50	0	fruit	1	0		0	18.25
Bulweria bulwerii	99.00	0	vertfishscav		0	cavity	0	1.34
Burhinus oedicnemus	451.00	0	invertebrate	1	1	open	0	3.38
Buteo buteo	859.63	0	vertfishscav	0	1	open	0	8.20
Buteo lagopus	910.12	0	vertfishscav	0	1	open	0	9.20
Buteo rufinus	1174.50	0	vertfishscav		1	open	0	9.17
Butorides striata	212.00	0	vertfishscav	0	1	open	0	2.48
Calcarius lapponicus	26.35	0	seed	1	1	open	0	0.87
Calidris alpina	45.29		invertebrate	1	1	open	0	1.00
Calidris canutus	137.00		invertebrate	1	1	open	0	1.32
Calidris ferruginea	60.30		invertebrate	1	1		0	0.99
Calidris maritima	72.42		invertebrate	1	1	open	0	1.05
Calidris melanotos	77.17		invertebrate	1	1	open	0	1.02
Calidris minuta	24.27		invertebrate	1	1	open	0	0.53
Calidris minutilla	27.10		invertebrate	1	1	open	0	0.51
Calidris ruficollis	29.30		invertebrate	1	1	open	0	0.66
Calidris tenuirostris	147.50		invertebrate	1	1		0	1.54

Species	Body Mass	Vocal Mimicry	Diet	Sociality	Migration	Nest Type	Parasitised	Brain Volume
Calonectris diomedea	571.80	0	vertfishscav	1	1	cavity	0	4.92
Caprimulgus europaeus	72.05	0	invertebrate	0	1	open	0	0.88
Caprimulgus macrurus	78.00	0	invertebrate		0		0	1.01
Carduelis cannabina	18.58	0	seed	1	1		0	0.64
Carduelis carduelis	15.14	0	seed	1	1	open	0	0.65
Carduelis chloris	26.65	0	seed	1	1	open	0	0.86
Carduelis flammea	12.75	0	seed	1	1		0	0.59
Carduelis flavirostris	14.85	0	seed	1	1		0	0.39
Carduelis spinus	12.46	0	seed	1	1	open	0	0.52
Carpodacus roseus	21.15	0	seed	1	1		0	0.97
Casmerodius albus	936.75	0	vertfishscav	0	1		0	5.04
Catharacta skua	1587.50		vertfishscav		1		0	7.24
Catharus minimus	32.80	0	invertebrate		1		0	0.77
Cepphus grylle	393.00		vertfishscav		1	open	0	3.61
Cerorhinca monocerata	487.50		vertfishscav		1	cavity	0	4.63
Certhia brachydactyla	8.40	1	invertebrate		0	cavity	0	0.51
Certhia familiaris	8.81	1	invertebrate	1	0	cavity	0	0.39
Ceryle rudis	84.40	0	vertfishscav		0	cavity	0	1.59
Charadrius alexandrinus	47.65	0	invertebrate	1	1	open	0	1.06
Charadrius dubius	38.75	0	invertebrate		1	open	0	0.75
Charadrius hiaticula	64.10	0	invertebrate	1	1	open	0	1.16
Charadrius leschenaultii	72.23	0	invertebrate	1	1	open	0	1.26

Species	Body Mass	Vocal Mimicry	Diet	Sociality	Migration	Nest Type	Parasitised	Brain Volume
Charadrius mongolus	63.70	0	invertebrate	0	1	open	0	1.13
Chlamydotis undulata	1360.00	0	omnivore		1	open	0	5.31
Chlidonias hybrida	88.20		invertebrate		1		0	1.48
Chlidonias leucopterus	80.10		invertebrate		1		0	1.35
Chrysolophus pictus	601.67	0	vegetation	1	0	open	0	3.34
Ciconia ciconia	3416.62	0	vertfishscav	1	1	open	0	14.67
Ciconia nigra	3000.00	0	vertfishscav		1	open	0	11.39
Cinclus cinclus	61.09	0	invertebrate	0	1	cave	0	1.30
Circus aeruginosus	600.75	0	vertfishscav		1	open	0	5.59
Circus cyaneus	379.50	0	vertfishscav	0	1	open	0	4.78
Cissa chinensis	116.65	1	invertebrate	1	0	open	0	3.45
Cisticola exilis	7.10	0	invertebrate	1	0		0	0.39
Coccothraustes coccothraustes	53.57	0	seed	1	1	open	0	1.60
Columba livia	320.38		seed	1	0	open	0	2.25
Columba palumbus	479.28		vegetation	1	1	open	0	2.31
Copsychus malabaricus	30.00	1	invertebrate		0		0	0.87
Copsychus saularis	33.20	1	invertebrate		0	cavity	0	1.10
Coracias garrulus	146.50	0	invertebrate		1	cavity	0	2.32
Corvus corax	1170.41	1	omnivore	1	1	open	0	14.55
Corvus corone	531.89	1	omnivore	1	1	open	1	8.95
Corvus dauuricus	123.00	0	omnivore	1	1		0	4.75
Corvus frugilegus	447.18	0	omnivore	1	1	open	0	7.61

Species	Body Mass	Vocal Mimicry	Diet	Sociality	Migration	Nest Type	Parasitised	Brain Volume
Corvus monedula	218.47	0	omnivore	1	1	cavity	0	4.87
Corvus ruficollis	741.25	0	omnivore	1	1		0	10.14
Corydon sumatranus	140.00	0	invertebrate	1	0		0	2.40
Coturnix coturnix	123.86	0	seed	1	1	open	0	0.88
Crex crex	151.39	0	omnivore	0	1	open	0	1.38
Cursorius cursor	133.75	0	invertebrate		1	open	0	1.44
Cyanopica cyanus	71.50	0	omnivore	1	0		1	2.44
Cygnus columbianus	6750.00	0	vegetation	1	1	open	0	17.35
Cygnus cygnus	9450.00	0	vegetation	1	1	open	0	19.50
Delichon urbicum	16.35	0	invertebrate	1	1	closed	0	0.48
Dendrocopos major	84.83	0	invertebrate	1	0		0	2.61
Dendrocopos medius	58.50	0	invertebrate	0	0		0	1.73
Dendrocopos minor	21.50	0	invertebrate	0	0		0	1.16
Dicrurus hottentottus	66.30	1	invertebrate	1	0		0	1.96
Dinopium javanense	78.50	0	invertebrate	1	0		0	2.67
Dryocopus martius	286.57	0	invertebrate	0	0	cavity	0	6.87
Ducula aenea	560.00	0	fruit	1	0		0	3.06
Emberiza aureola	21.15	0	seed	1	1	open	0	0.69
Emberiza cirlus	23.43	0	seed	1	0	open	0	0.76
Emberiza citrinella	29.14	0	seed	1	1	open	0	0.77
Emberiza hortulana	23.80	0	seed	1	1	open	0	0.70
Emberiza melanocephala	28.35	0	seed	1	1	open	0	0.71

Species	Body Mass	Vocal Mimicry	Diet	Sociality	Migration	Nest Type	Parasitised	Brain Volume
Emberiza schoeniclus	19.72	0	seed	1	1	open	0	0.68
Emberiza spodocephala	18.00	0	seed	1	1	open	0	0.93
Eremophila alpestris	34.80	0	seed	1	1	open	1	0.89
Eremophila bilopha	31.02	0	seed	1	0		1	0.82
Eremopsaltria mongolicus	21.90	0	seed	1	1		0	0.65
Erithacus rubecula	17.24	1	invertebrate	0	1	open	0	0.62
Estrilda astrild	7.50	0	seed	1	0		1	0.34
Eurostopodus macrotis	168.80	0	invertebrate		0		0	1.46
Eurystomus orientalis	131.00	0	invertebrate	1	1		0	1.98
Falco biarmicus	700.00	0	vertfishscav		1	open	0	6.08
Falco eleonorae	385.00	0	invertebrate		1	cave	0	4.04
Falco naumanni	155.25	0	invertebrate	1	1	cave	0	2.71
Falco peregrinus	729.25	0	vertfishscav	0	1	open	0	6.19
Falco rusticolus	1425.00	0	vertfishscav	0	1	open	0	7.72
Falco subbuteo	210.00	0	invertebrate		1	open	0	3.59
Falco tinnunculus	209.49	0	vertfishscav	0	1	cave	0	3.71
Falco vespertinus	158.25	0	invertebrate		1	open	0	2.70
Ficedula albicollis	10.30	0	invertebrate		1	cavity	0	0.45
Ficedula hypoleuca	12.38	0	invertebrate	0	1	cavity	0	0.40
Fratercula arctica	385.38		vertfishscav	1	1	cavity	0	4.05
Fratercula cirrhata	779.00		vertfishscav		1		0	5.69
Fratercula corniculata	641.10		vertfishscav		1	cavity	0	5.19

Species	Body Mass	Vocal Mimicry	Diet	Sociality	Migration	Nest Type	Parasitised	Brain Volume
Fringilla coelebs	22.31	0	omnivore	1	1		0	0.81
Fringilla montifringilla	23.80	0	seed	1	1	open	1	0.71
Fulica atra	557.46	0	vegetation	1	1	open	0	2.85
Fulmarus glacialis	619.80	0	vertfishscav	1	1	open	0	6.33
Galerida theklae	35.60	1	invertebrate	1	0		1	0.89
Gallinago gallinago	100.31		invertebrate	1	1	open	0	1.41
Gallinago media	165.00		invertebrate	1	1		0	2.03
Gallus gallus	1331.00	0	omnivore	1	0		0	2.94
Gallus sonneratii	717.00	0	omnivore	1	0		0	3.21
Garrulax leucolophus	123.50	0	invertebrate	1	0		1	2.46
Garrulus glandarius	165.14	1	omnivore	1	0	open	0	3.87
Gavia arctica	2804.50	0	vertfishscav		1	open	0	7.24
Gavia stellata	1520.50	0	vertfishscav	1	1	open	0	5.54
Geronticus eremita	1200.00	0	vertfishscav	1	1	open	0	7.92
Glaucidium passerinum	58.50	0	vertfishscav		0	cavity	0	2.59
Gracula religiosa	192.00	1	fruit	1	0		1	3.68
Grus antigone	8181.50	0	omnivore	1	1	open	0	20.06
Grus canadensis	3901.10	0	omnivore	1	1	open	0	14.82
Grus grus	5148.75	0	omnivore		1	open	0	16.99
Grus virgo	2154.00	0	seed	1	1		0	10.23
Gypaetus barbatus	5543.75	0	vertfishscav		0	cave	0	23.26
Haematopus ostralegus	509.00	0	invertebrate	1	1	open	0	3.65

Species	Body Mass	Vocal Mimicry	Diet	Sociality	Migration	Nest Type	Parasitised	Brain Volume
Halcyon smyrnensis	85.30	0	invertebrate		1		0	1.84
Haliaeetus albicilla	4793.00	0	vertfishscav		1	open	0	18.34
Haliaeetus leucogaster	3004.00	0	vertfishscav	1	0	open	0	12.59
Haliastur indus	530.00	0	vertfishscav		0		0	6.10
Heteroscelus incanus	109.00		invertebrate	1	1		0	1.29
Hieraaetus pennatus	820.00	0	vertfishscav	1	1	open	0	5.31
Himantopus mexicanus	168.90	0	invertebrate	1	1		0	1.90
Hippolais icterina	13.35	1	invertebrate		1	open	0	0.47
Hirundo rustica	17.89	0	invertebrate	1	1	cave	0	0.54
Histrionicus histrionicus	611.30	0	invertebrate	1	1	open	0	4.86
Hydrophasianus chirurgus	178.50	0	invertebrate	1	1	open	0	1.40
Hypothymis azurea	10.20	0	invertebrate	1	0		0	0.52
Irania gutturalis	24.40	1	invertebrate		1		0	0.63
Irena puella	62.38	0	fruit		0		1	1.36
Ixobrychus minutus	141.75	0	invertebrate	0	1	open	0	1.54
Jynx torquilla	34.66	0	invertebrate	0	1	cavity	0	0.94
Lagopus lagopus	572.51	0	vegetation		1	open	0	2.38
Lanius collurio	29.69	0	invertebrate	0	1	open	0	0.96
Lanius cristatus	29.70	1	invertebrate	0	1		1	1.05
Lanius excubitor	61.52	1	vertfishscav	0	1	open	1	1.57
Lanius senator	27.80	1	invertebrate	0	1	open	0	1.07
Larus argentatus	995.00	0	omnivore	1	1	open	0	5.50

Species	Body Mass	Vocal Mimicry	Diet	Sociality	Migration	Nest Type	Parasitised	Brain Volume
Larus canus	383.52		invertebrate	1	1	open	0	4.10
Larus fuscus	817.50		vertfishscav		1	open	0	5.50
Larus glaucescens	1408.90		omnivore	1	1	open	0	7.62
Larus hyperboreus	1412.50		omnivore		1	open	0	7.72
Larus marinus	1638.25		omnivore	1	1	open	0	7.20
Larus minutus	98.50	0	invertebrate		1	open	0	1.83
Larus ridibundus	265.89		invertebrate	1	1	open	0	2.88
Leiothrix argentauris	26.20	0	invertebrate	1	0		0	0.94
Leiothrix lutea	21.80	0	omnivore	1	0		0	0.92
Limicola falcinellus	34.20		invertebrate	1	1	open	0	0.72
Limosa lapponica	323.40		invertebrate	1	1	open	0	2.77
Limosa limosa	289.50		invertebrate	1	1	open	0	2.80
Locustella fluviatilis	18.80	0	invertebrate		1		0	0.43
Locustella luscinioides	15.00	0	invertebrate		1	open	0	0.55
Locustella naevia	11.80	0	invertebrate		1	open	0	0.58
Lonchura malacca	12.60	0	seed	1	0		0	0.60
Lonchura striata	12.30	0	seed	1	0		0	0.60
Loxia curvirostra	37.72	0	seed	1	0	open	0	1.42
Loxia leucoptera	32.30	0	seed	1	1	open	0	1.38
Loxia pytyopsittacus	54.40	0	seed	1	1		0	1.76
Luscinia luscinia	25.00	1	invertebrate	0	1		0	0.72
Luscinia megarhynchos	19.40	0	invertebrate		1		0	0.70

Species	Body Mass	Vocal Mimicry	Diet	Sociality	Migration	Nest Type	Parasitised	Brain Volume
Luscinia svecica	21.60	1	invertebrate		1		0	0.66
Megalaima asiatica	98.90	0	fruit	0	0		0	1.58
Megalaima zeylanica	105.80	0	fruit		0		0	1.90
Megalurus palustris	33.30	0	invertebrate	1	0		1	1.14
Melanitta fusca	1829.00	0	invertebrate	1	1	open	0	7.14
Melanitta nigra	1047.37	0	invertebrate	1	1	open	0	5.68
Melanocorypha calandra	58.20	1	seed	1	0	open	0	1.31
Merops apiaster	57.23	0	invertebrate	1	1	cavity	0	0.88
Merops orientalis	14.80	0	invertebrate		1	cavity	0	0.48
Mesophoyx intermedia	500.00	0	vertfishscav	0	0		0	4.15
Miliaria calandra	46.65	0	seed	1	1	open	0	1.14
Milvus migrans	712.00	0	vertfishscav		1	open	0	5.82
Milvus milvus	1121.90	0	vertfishscav		1	open	0	7.05
Monticola saxatilis	48.50	1	invertebrate		1	cave	0	1.29
Monticola solitarius	47.30	1	invertebrate		1	cave	0	1.32
Montifringilla nivalis	39.30	0	seed	1	0		0	1.05
Morus bassanus	2999.50	0	vertfishscav	1	0	open	0	18.53
Motacilla alba	21.78	0	invertebrate	1	1	cave	0	0.60
Motacilla cinerea	17.35	0	invertebrate		1	cave	0	0.51
Motacilla flava	15.93	0	invertebrate	1	1	open	1	0.55
Muscicapa striata	15.53	0	invertebrate	1	1	open	0	0.49
Nectarinia jugularis	8.70	0	nectar	1	0	closed	1	0.40

Species	Body Mass	Vocal Mimicry	Diet	Sociality	Migration	Nest Type	Parasitised	Brain Volume
Neophron percnopterus	1977.00	0	vertfishscav		1	cave	0	10.62
Nucifraga caryocatactes	191.24	0	seed	1	0	open	0	5.41
Numenius arquata	687.50		invertebrate	1	1	open	0	3.90
Numenius phaeopus	381.25		invertebrate	0	1	open	0	3.13
Nycticorax nycticorax	756.05	0	vertfishscav	0	1	open	0	6.66
Oceanodroma leucorhoa	44.95	0	vertfishscav	1	0	cavity	0	0.89
Oena capensis	40.60		seed	1	1	open	0	0.61
Oenanthe oenanthe	24.18	1	invertebrate	0	1	cave	1	0.78
Oriolus oriolus	71.65	0	invertebrate	1	1	open	1	1.36
Otis tarda	7895.50	0	omnivore		1	open	0	10.42
Otus scops	84.55	0	invertebrate	0	1	cavity	0	2.49
Pandion haliaetus	1504.33	0	vertfishscav	1	1		0	9.38
Panurus biarmicus	14.62	0	invertebrate	1	1	open	0	0.53
Parus ater	8.84	0	invertebrate	1	0	cavity	0	0.54
Parus caeruleus	11.45	0	invertebrate	1	0		0	0.62
Parus cristatus	10.62	0	invertebrate	1	1	cavity	0	0.66
Parus cyanus	11.25	0	invertebrate	1	0		0	0.64
Parus major	17.84	0	invertebrate	1	1	cavity	0	0.88
Parus montanus	11.62	0	invertebrate	1	0	cavity	0	0.76
Parus palustris	11.50	0	invertebrate	1	0	cavity	0	0.64
Parus venustulus	10.54	0	invertebrate	1	0		0	0.51
Passer hispaniolensis	26.34	0	seed	1	1	closed	0	0.97

Species	Body Mass	Vocal Mimicry	Diet	Sociality	Migration	Nest Type	Parasitised	Brain Volume
Passer montanus	21.74	0	seed	1	0	cavity	0	0.75
Pelargopsis capensis	170.00	0	vertfishscav		0		0	2.82
Pelecanus onocrotalus	9260.00	0	vertfishscav	1	1	open	0	31.85
Pericrocotus ethologus	18.00	0	invertebrate	1	1		0	0.88
Pernis apivorus	762.50	0	invertebrate	0	1	open	0	7.38
Phaethon rubricauda	672.00	0	vertfishscav		1	open	0	4.52
Phalacrocorax carbo	2405.83	0	vertfishscav	1	1	open	0	10.45
Phalacrocorax pygmeus	700.00	0	vertfishscav	1	1		0	4.54
Phalacrocorax urile	2181.40	0	vertfishscav		0	open	0	8.22
Phalaropus fulicarius	52.65		invertebrate	1	1		0	0.56
Phalaropus lobatus	35.30		invertebrate	1	1	open	0	0.45
Philomachus pugnax	158.67		invertebrate	1	1	open	0	1.56
Phoebastria nigripes	3148.00	0	vertfishscav		1	open	0	15.80
Phoenicurus ochruros	16.12	1	invertebrate		1	cave	0	0.60
Phoenicurus phoenicurus	14.73	1	invertebrate		1	cavity	1	0.51
Phylloscopus bonelli	7.40	0	invertebrate	1	1		0	0.34
Phylloscopus collybita	7.77	0	invertebrate	1	1	closed	0	0.34
Phylloscopus sibilatrix	7.20	0	invertebrate	1	1	closed	0	0.36
Phylloscopus trochilus	9.32	1	invertebrate	1	1	closed	0	0.31
Pica pica	204.98	1	omnivore	1	1	closed	1	4.67
Picoides tridactylus	55.20	0	invertebrate	0	0	cavity	0	2.63
Picus canus	136.30	0	invertebrate	0	0	cavity	0	3.68

Species	Body Mass	Vocal Mimicry	Diet	Sociality	Migration	Nest Type	Parasitised	Brain Volume
Picus viridis	191.92	0	invertebrate	0	0	cavity	0	4.23
Pinicola enucleator	65.70	1	seed	1	1	open	0	1.58
Pitta brachyura	55.50	0	invertebrate		1		0	1.39
Pitta sordida	57.55	0	invertebrate		1		0	1.31
Platalea leucorodia	1261.50	0	invertebrate	1	1	open	0	10.42
Plectrophenax nivalis	34.80	0	seed	1	1	cave	0	1.02
Plegadis falcinellus	623.33	0	invertebrate	1	1	open	0	5.12
Pluvialis apricaria	193.97	0	invertebrate	1	1	open	0	2.23
Pluvialis squatarola	219.93	0	invertebrate	1	1	open	0	2.56
Podiceps auritus	445.60	0	vertfishscav	1	1	open	0	2.43
Podiceps cristatus	892.99	0	vertfishscav	1	1	open	0	3.11
Podiceps grisegena	972.23	0	invertebrate	1	1	open	0	4.04
Podiceps nigricollis	292.00	0	invertebrate	1	1	open	0	1.69
Polysticta stelleri	869.50	0	invertebrate	1	1	open	0	5.28
Porphyrio porphyrio	765.30	0	vegetation	1	0	open	0	4.70
Porzana porzana	80.40	0	omnivore	1	1	open	0	1.16
Prunella collaris	39.55	0	invertebrate	1	0	open	0	0.94
Prunella modularis	19.93		invertebrate	0	1	open	1	0.78
Psittacula krameri	137.00		fruit		0		0	4.07
Puffinus griseus	770.00	0	vertfishscav	1	1	cavity	0	5.31
Puffinus pacificus	383.40	0	vertfishscav		1	cavity	0	3.97
Puffinus puffinus	453.00	0	vertfishscav	1	1	cavity	0	3.43

Species	Body Mass	Vocal Mimicry	Diet	Sociality	Migration	Nest Type	Parasitised	Brain Volume
Puffinus tenuirostris	534.47	0	vertfishscav	1	1	cavity	0	4.64
Pycnonotus barbatus	35.90	0	fruit	1	0		1	1.13
Pycnonotus jocosus	27.40	0	fruit	1	0	open	0	0.93
Pyrrhocorax graculus	191.71	0	omnivore	1	0	cave	0	3.09
Pyrrhocorax pyrrhocorax	311.58	0	invertebrate	1	0	cave	1	6.38
Pyrrhula pyrrhula	26.43	0	seed	1	1	open	0	0.89
Rallus aquaticus	113.16	0	omnivore	1	1	open	0	1.73
Recurvirostra avosetta	306.00	0	invertebrate		1	open	0	1.93
Regulus regulus	5.63	0	invertebrate	1	1	closed	0	0.34
Remiz pendulinus	9.15	1	invertebrate	1	1	cavity	0	0.43
Rhodostethia rosea	223.40	0	invertebrate	1	1	open	0	2.15
Rissa brevirostris	391.00	0	omnivore		1	open	0	4.17
Rissa tridactyla	446.70	0	invertebrate	1	1	open	0	4.31
Rostratula benghalensis	149.50	0	omnivore	0	1	open	0	1.42
Sarkidiornis melanotos	1776.30	0	vegetation		0		0	6.99
Saxicola rubetra	16.25	1	invertebrate		1	open	0	0.62
Saxicola torquatus	15.30	1	invertebrate	0	1	open	1	0.61
Scolopax rusticola	305.03		invertebrate	0	1	open	0	2.50
Serinus serinus	11.57	0	seed	1	1		0	0.52
Sitta europaea	23.11	0	invertebrate	1	0	cavity	0	1.02
Sitta neumayer	32.25	0	invertebrate	1	0		0	1.12
Somateria spectabilis	1638.90	0	invertebrate	1	1	open	0	7.39

Species	Body Mass	Vocal Mimicry	Diet	Sociality	Migration	Nest Type	Parasitised	Brain Volume
Stercorarius parasiticus	470.30		vertfishscav		1	open	0	3.89
Stercorarius pomarinus	544.80		vertfishscav	1	1	open	0	4.79
Sterna albifrons	48.75		vertfishscav	1	1	open	0	0.87
Sterna bergii	342.00		vertfishscav	1			0	3.36
Sterna fuscata	185.50		omnivore		1	open	0	2.32
Sterna hirundo	113.67		vertfishscav	1	1	open	0	1.74
Sterna paradisaea	112.25		vertfishscav	1	1	open	0	2.00
Sterna sandvicensis	250.00		vertfishscav	1	1		0	2.70
Stigmatopelia chinensis	161.50	0	seed	1	0		0	1.35
Stigmatopelia senegalensis	101.20		seed	1	0	open	0	1.24
Streptopelia decaocto	184.26	0	seed	1	0	open	0	1.40
Streptopelia roseogrisea	143.50		fruit	1	1		0	1.10
Streptopelia turtur	140.80	0	seed		1	open	0	1.39
Strix aluco	445.63	0	vertfishscav	0	0	cavity	0	9.08
Strix nebulosa	1067.45	0	vertfishscav		1	open	0	14.66
Strix uralensis	784.50	0	vertfishscav		1	cavity	0	11.21
Sula leucogaster	1237.50	0	vertfishscav	0	1	open	0	9.04
Sylvia atricapilla	18.50	0	invertebrate		1	open	0	0.65
Sylvia borin	17.83	1	invertebrate	0	1	open	1	0.62
Sylvia communis	14.29	1	invertebrate		1	open	1	0.52
Sylvia curruca	12.61	0	invertebrate		1	open	0	0.50
Sylvia hortensis	22.40	0	invertebrate		1	open	0	0.71

Species	Body Mass	Vocal Mimicry	Diet	Sociality	Migration	Nest Type	Parasitised	Brain Volume
Sylvia melanocephala	11.34	0	invertebrate	0	1		0	0.51
Sylvia nisoria	22.80	0	invertebrate		1	open	0	0.69
Synthliboramphus antiquus	206.00		invertebrate	1	1	cavity	0	2.43
Tachybaptus ruficollis	144.47	0	invertebrate	0	1	open	0	1.56
Tachymarptis melba	95.00	0	invertebrate	1	1		0	1.09
Tadorna tadorna	1076.85	0	invertebrate		1	cavity	0	5.33
Tephrodornis pondicerianus	19.50	0	invertebrate	1	0	open	0	0.89
Tetrao tetrix	1194.50	0	vegetation	1	0	open	0	3.40
Tetrao urogallus	3056.25	0	vegetation	1	0	open	0	6.14
Threskiornis aethiopicus	1498.00	0	invertebrate	1	1	open	0	10.24
Tichodroma muraria	16.00	0	invertebrate	0	1	cavity	0	0.44
Todiramphus chloris	61.95	0	invertebrate		0		0	1.34
Tringa erythropus	151.50		invertebrate	1	1	open	0	1.74
Tringa glareola	67.50		invertebrate	0	1	open	0	1.04
Tringa nebularia	163.01		invertebrate	1	1	open	0	1.66
Tringa ochropus	80.00		invertebrate	0	1	open	0	1.25
Tringa totanus	116.62		invertebrate	1	1	open	0	1.32
Troglodytes troglodytes	9.39	0	invertebrate	0	1	closed	1	0.49
Turdus iliacus	62.85	0	invertebrate		1	open	0	1.28
Turdus merula	100.16	1	invertebrate	1	1	open	0	1.82
Turdus philomelos	68.81	0	invertebrate		1	open	0	1.63
Turdus torquatus	107.75	0	invertebrate		1	open	0	1.67

Species	Body Mass	Vocal Mimicry	Diet	Sociality	Migration	Nest Type	Parasitised	Brain Volume
Turdus viscivorus	117.80	1	invertebrate		1	open	0	2.31
Turnix suscitator	56.30	0	seed	1	1		0	0.71
Tyto alba	358.22	0	vertfishscav	0	0	cavity	0	6.41
Tyto longimembris	478.00	0	vertfishscav		0		0	5.25
Upupa epops	55.36	0	invertebrate	0	1	cavity	0	1.35
Uria aalge	918.60		vertfishscav	1	1	open	0	5.73
Uria lomvia	967.35		vertfishscav	1	1	open	0	5.30
Urocissa erythrorhyncha	208.35	1	omnivore	1	0		0	3.67
Vanellus vanellus	211.58		invertebrate	1	1	open	0	2.13
Xema sabini	190.20	0	invertebrate	1	1	open	0	2.21
Xenus cinereus	72.00		invertebrate	1	1		0	1.03
Zosterops japonicus	10.20	1	invertebrate		1		1	0.54

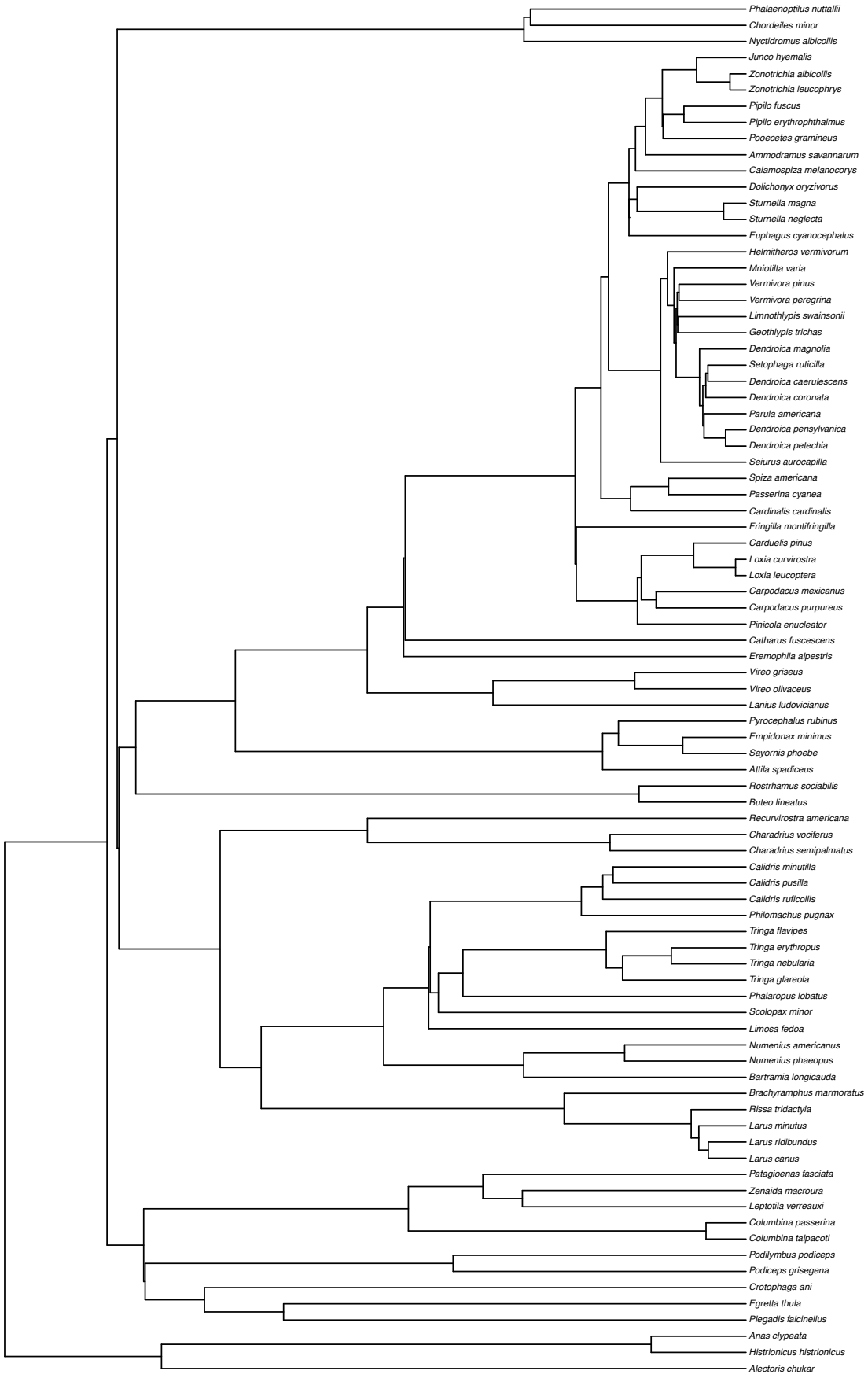

Figure 1.7: Example phylogeny of potential cowbird hosts from a block of 1000 avian trees (Jetz et al 2012).

Table 1.15: Phenotypic data on brain size, body mass, nest type, diet, vocal mimicry, sociality, migration and whether or not a species is parasitised in species with breeding ranges overlapping that of the brown-headed cowbird (*Molothrus ater).*

Species	Body Mass	Vocal Mimicry	Diet	Sociality	Migration	Nest Type	Parasitised	Brain Volume
Podilymbus podiceps	442.00	0	invertebrate	1	1	open	0	3.16
Accipiter cooperii	323.20	0	vertfishscav	0	1	open	0	4.70
Accipiter gentilis	936.32	0	vertfishscav	0	1	open	0	7.88
Accipiter striatus	118.00	0	vertfishscav	0	1	open	0	2.23
Acridotheres tristis	115.60	1	omnivore	1	0	cavity	1	2.48
Actitis macularius	45.40		invertebrate	0	1		0	0.68
Aechmophorus occidentalis	1147.70	0	vertfishscav	1	1	open	0	3.71
Aegolius acadicus	95.15	0	vertfishscav	0	1	cavity	0	2.85
Aegolius funereus	91.20	0	vertfishscav		0	cavity	0	4.02
Agelaius phoeniceus	60.13	0	omnivore	1	0	open	1	1.69
Aimophila cassinii	18.10	0	invertebrate	1	1		1	0.78
Alca torda	720.67		vertfishscav	1	1	open	0	5.38
Alectoris chukar	536.33	0	seed	1	0	open	0	2.49
Amazona finschi	298.00	0		1			0	7.64
Ammodramus savannarum	17.00	0	invertebrate	0	1	open	1	0.65
Amphispiza bilineata	13.80	0	seed	1	1		1	0.68
Anas acuta	894.75	0	omnivore	1	1	open	1	4.72
Anas americana	734.10	0	vegetation	1	1	open	0	4.05

Species	Body Mass	Vocal Mimicry	Diet	Sociality	Migration	Nest Type	Parasitised	Brain Volume
Anas clypeata	577.95	0	invertebrate	1	1	open	1	3.42
Anas crecca	322.50	0	vegetation	1	1	open	0	2.55
Anas discors	366.60	0	vegetation	1	1	open	1	2.91
Aphelocoma coerulescens	75.72	0	omnivore	1	0	open	0	2.85
Aphelocoma ultramarina	121.20	0	omnivore	1	0		0	3.61
Aquila chrysaetos	4484.38	0	vertfishscav	1	1	open	0	17.19
Aramus guarauna	1080.00	0	invertebrate	1	0		0	6.62
Archilochus colubris	3.30	0	nectar	0	1	open	0	0.15
Ardea herodias	2295.00	0	vertfishscav	0	1	open	0	8.88
Asio flammeus	329.84	0	vertfishscav	0	0	open	0	5.30
Asio otus	249.67	0	vertfishscav	0	1	open	0	5.32
Athene cunicularia	159.90	0	vertfishscav	0	1	cavity	0	4.82
Attila spadiceus	33.20	0	invertebrate	1	0	open	0	1.18
Auriparus flaviceps	6.60	0	invertebrate	1	0	cavity	0	0.44
Aythya collaris	717.30	0	vegetation	1	1	open	1	5.38
Baeolophus bicolor	21.60	0	invertebrate	1	0	cavity	0	1.01
Bartramia longicauda	159.00		invertebrate	1	1	open	0	1.30
Bombycilla cedrorum	33.70	0	fruit	1	1	open	0	0.89
Bombycilla garrulus	55.78	0	fruit	1	1	open	0	1.13
Bonasa umbellus	597.90	0	vegetation		0	open	0	2.80
Botaurus lentiginosus	706.00	0	vertfishscav	0	1	open	0	4.52
Brachyramphus marmoratus	233.40		invertebrate	1	1	open	0	2.35

Species	Body Mass	Vocal Mimicry	Diet	Sociality	Migration	Nest Type	Parasitised	Brain Volume
Bubo virginianus	1415.87	0	vertfishscav		0		0	16.36
Buteo jamaicensis	1053.90	0	vertfishscav	0	1	open	0	9.18
Buteo lagopus	910.12	0	vertfishscav	0	1	open	0	9.20
Buteo lineatus	606.90	0	invertebrate	0	1	open	0	7.19
Buteo magnirostris	334.60	0	invertebrate		0		0	4.56
Buteo platypterus	397.00	0	vertfishscav	0	1	open	0	5.12
Buteo regalis	1469.50	0	vertfishscav	1	1		0	9.50
Buteo swainsoni	899.00	0	vertfishscav	1	1		0	7.73
Buteogallus anthracinus	923.80	0	vertfishscav	1	0		0	7.17
Buteogallus urubitinga	1141.10	0	vertfishscav	1	0		0	10.17
Butorides striata	212.00	0	vertfishscav	0	1	open	0	2.48
Cairina moschata	2625.00	0	omnivore	1	0		0	7.35
Calamospiza melanocorys	37.80	0	seed	1	1	open	1	1.18
Calidris ferruginea	60.30		invertebrate	1	1		0	0.99
Calidris minutilla	27.10		invertebrate	1	1	open	0	0.51
Calidris pusilla	26.75		invertebrate	1	1	open	0	0.51
Calidris ruficollis	29.30		invertebrate	1	1	open	0	0.66
Callipepla californica	174.20	0	seed		0		0	1.33
Calypte anna	8.55	0	nectar		0	open	0	0.18
Campephilus guatemalensis	240.70	0	invertebrate	1	0		0	5.94
Campylorhynchus brunneicapillus	38.90	0	invertebrate		0	closed	0	1.34

Species	Body Mass	Vocal Mimicry	Diet	Sociality	Migration	Nest Type	Parasitised	Brain Volume
Caprimulgus carolinensis	109.20	0	invertebrate	0	1		0	1.36
Caprimulgus vociferus	50.80	0	invertebrate	0	1		0	0.82
Caracara cheriway	893.50	0	invertebrate		0		0	9.26
Cardellina rubrifrons	9.80	0	invertebrate	0	1		1	0.43
Cardinalis cardinalis	44.10	0	seed	1	0	open	1	1.52
Carduelis flammea	12.75	0	seed	1	1		0	0.59
Carduelis pinus	13.68	0	seed	1	1	open	1	0.57
Carduelis tristis	12.70	0	seed	1	1		1	0.54
Carpodacus mexicanus	20.40	0	seed	1	0	open	1	0.78
Carpodacus purpureus	25.60	1	seed	1	1	open	1	0.90
Casmerodius albus	936.75	0	vertfishscav	0	1		0	5.04
Cathartes aura	1733.30	0	vertfishscav	1	1	cavity	0	9.98
Catharus fuscescens	41.50	0	invertebrate	0	1	open	1	0.92
Catharus guttatus	38.12	0	invertebrate	1	1		1	0.93
Catharus minimus	32.80	0	invertebrate		1		0	0.77
Catharus ustulatus	30.80	0	invertebrate	1	1		1	0.79
Centrocercus urophasianus	2195.90	0	vegetation		0	open	0	4.00
Cepphus grylle	393.00		vertfishscav		1	open	0	3.61
Cerorhinca monocerata	487.50		vertfishscav		1	cavity	0	4.63
Chaetura pelagica	22.30	0	invertebrate	1	1	cavity	0	0.40
Chamaea fasciata	14.70	0	invertebrate	1	0		1	0.77
Charadrius semipalmatus	47.00	0	invertebrate	1	1	open	0	0.96

Species	Body Mass	Vocal Mimicry	Diet	Sociality	Migration	Nest Type	Parasitised	Brain Volume
Charadrius vociferus	92.75	0	invertebrate	1	1	open	0	1.10
Chlidonias hybrida	88.20		invertebrate		1		0	1.48
Chloroceryle americana	37.50	0	vertfishscav		0		0	0.92
Chordeiles minor	68.20	0	invertebrate	1	1	open	0	0.85
Cinclus mexicanus	57.80	0	invertebrate		0	cave	0	1.40
Cistothorus palustris	10.00	0	invertebrate	1	1	closed	0	0.52
Coccothraustes vespertinus	57.20	1	seed	1	1		0	1.70
Cochlearius cochlearius	657.00	0	vertfishscav		0		0	5.83
Colaptes auratus	152.80	0	invertebrate	1	1		0	3.06
Columbina inca	45.25	0	seed	1	0		0	0.73
Columbina passerina	33.30	0	seed	1	0	open	0	0.64
Columbina talpacoti	47.10	0	seed	1	1	open	0	0.72
Contopus cooperi	32.80	0	invertebrate		1		0	0.64
Contopus virens	14.20	0	invertebrate	0	1		0	0.45
Coragyps atratus	2080.50	0	vertfishscav	1	0	cave	0	11.99
Corvus brachyrhynchos	438.50	1	omnivore	1	1	open	0	7.17
Corvus caurinus	384.00	0	omnivore	1	0	open	0	7.43
Corvus corax	1170.41	1	omnivore	1	1	open	0	14.55
Corvus cryptoleucus	534.00	0	omnivore	1	1	open	0	8.95
Corvus ossifragus	285.00	0	omnivore	1	1	open	0	5.99
Coturnicops noveboracensis	55.70	0	invertebrate	0	1		0	0.74
Crotophaga ani	100.20	0	invertebrate	1	0	open	0	1.56

Species	Body Mass	Vocal Mimicry	Diet	Sociality	Migration	Nest Type	Parasitised	Brain Volume
Cyanocitta cristata	95.67	1	omnivore	1	1	open	0	2.92
Cyanocitta stelleri	128.00	1	omnivore	1	0	open	0	3.54
Cyanocorax morio	204.00	0	omnivore	1	0		0	4.80
Cyanocorax yncas	78.50	1	omnivore	1	0		0	2.32
Cygnus buccinator	10863.00	0	vegetation	1	1		0	20.29
Dendragapus canadensis	520.80	0	vegetation	1	0		0	2.44
Dendragapus obscurus	1009.80	0	vegetation	1	0	open	0	3.07
Dendroica caerulescens	9.40	0	invertebrate	0	1	open	1	0.43
Dendroica castanea	12.00	0	invertebrate	1	1		0	0.40
Dendroica coronata	12.50	0	invertebrate	1	1	open	1	0.51
Dendroica magnolia	8.45	0	invertebrate	0	1	open	1	0.37
Dendroica pensylvanica	9.40	0	invertebrate	1	1	open	1	0.38
Dendroica petechia	9.80	0	invertebrate	1	1	open	1	0.52
Dolichonyx oryzivorus	38.70	0	invertebrate	1	1	open	0	1.07
Dryocopus pileatus	282.80	0	invertebrate	0	0		0	6.80
Dumetella carolinensis	39.25	1	omnivore	0	1	open	0	1.14
Egretta thula	382.50	0	invertebrate	1	1	open	0	3.61
Empidonax minimus	10.50	0	invertebrate	0	1	open	1	0.37
Empidonax oberholseri	12.27	0	invertebrate		1		1	0.41
Empidonax virescens	12.90	0	invertebrate		1		1	0.43
Eremophila alpestris	34.80	0	seed	1	1	open	1	0.89
Eudocimus albus	900.00	0	invertebrate	1	0		0	6.36

Species	Body Mass	Vocal Mimicry	Diet	Sociality	Migration	Nest Type	Parasitised	Brain Volume
Euphagus cyanocephalus	68.50	0	invertebrate	1	1	open	1	1.44
Falco columbarius	172.20	0	vertfishscav	0	1	open	0	3.09
Falco mexicanus	638.40	0	vertfishscav	0	1	open	0	6.86
Falco peregrinus	729.25	0	vertfishscav	0	1	open	0	6.19
Falco rufigularis	168.80	0	vertfishscav		0		0	3.18
Falco sparverius	92.00	0	invertebrate	0	1	cavity	0	2.49
Fratercula arctica	385.38		vertfishscav	1	1	cavity	0	4.05
Fratercula cirrhata	779.00		vertfishscav		1		0	5.69
Fringilla montifringilla	23.80	0	seed	1	1	open	1	0.71
Fulmarus glacialis	619.80	0	vertfishscav	1	1	open	0	6.33
Gavia immer	4036.90	0	vertfishscav	1	1	open	0	10.10
Gavia stellata	1520.50	0	vertfishscav	1	1	open	0	5.54
Geococcyx californianus	302.70	0	invertebrate	1	0		0	3.49
Geothlypis trichas	9.60	0	invertebrate	0	1	open	1	0.52
Glaucidium brasilianum	68.70	0	invertebrate		0		0	2.51
Glaucidium gnoma	61.90	0	invertebrate		0	cavity	0	3.60
Grus canadensis	3901.10	0	omnivore	1	1	open	0	14.82
Gymnorhinus cyanocephalus	102.67	0	omnivore	1	1		0	3.51
Haematopus palliatus	602.50	0	invertebrate	1	0		0	4.52
Haliaeetus leucocephalus	4418.95	0	vertfishscav	1	1	open	0	18.04
Helmitheros vermivorum	14.20	0	invertebrate	0	1	open	1	0.59
Herpetotheres cachinnans	621.00	0	vertfishscav		0		0	6.55

Species	Body Mass	Vocal Mimicry	Diet	Sociality	Migration	Nest Type	Parasitised	Brain Volume
Himantopus mexicanus	168.90	0	invertebrate	1	1		0	1.90
Hirundo rustica	17.89	0	invertebrate	1	1	cave	0	0.54
Histrionicus histrionicus	611.30	0	invertebrate	1	1	open	0	4.86
Hylocichla mustelina	47.40	0	invertebrate	1	1		1	1.25
Icteria virens	24.90	0	invertebrate	0	1		1	0.91
Icterus galbula	33.30	0	invertebrate	1	1		1	1.13
Icterus spurius	20.40	0	invertebrate	1	1		1	0.86
Ictinia mississippiensis	278.00	0	invertebrate	1	1		0	3.69
Ixobrychus exilis	80.40	0	vertfishscav	0	1	open	1	1.28
Jacana spinosa	118.00	0	invertebrate		0		0	1.38
Junco hyemalis	18.90	0	seed	1	1	open	1	0.83
Lagopus lagopus	572.51	0	vegetation		1	open	0	2.38
Lanius excubitor	61.52	1	vertfishscav	0	1	open	1	1.57
Lanius ludovicianus	47.40	0	invertebrate	0	1	open	1	1.53
Larus canus	383.52		invertebrate	1	1	open	0	4.10
Larus delawarensis	508.20		vertfishscav	1	1	open	0	4.44
Larus dominicanus	968.00		omnivore		1	open	0	6.61
Larus glaucescens	1408.90		omnivore	1	1	open	0	7.62
Larus glaucoides	900.00		vertfishscav		1	open	0	7.24
Larus marinus	1638.25		omnivore	1	1	open	0	7.20
Larus minutus	98.50	0	invertebrate		1	open	0	1.83
Larus ridibundus	265.89		invertebrate	1	1	open	0	2.88

Species	Body Mass	Vocal Mimicry	Diet	Sociality	Migration	Nest Type	Parasitised	Brain Volume
Leptotila verreauxi	127.70	0	seed		0	open	0	1.42
Limnothlypis swainsonii	14.00	0	invertebrate	1	1	open	1	0.67
Limosa fedoa	343.00		invertebrate	1	1	open	0	2.73
Loxia curvirostra	37.72	0	seed	1	0	open	0	1.42
Loxia leucoptera	32.30	0	seed	1	1	open	0	1.38
Megaceryle alcyon	147.80	0	vertfishscav	0	1		0	2.03
Megaceryle torquata	317.00	0	vertfishscav		0		0	3.57
Megascops asio	180.25	0	vertfishscav		0		0	4.91
Melanerpes carolinus	72.50	0	omnivore	0	1	cavity	0	2.16
Melanerpes erythrocephalus	70.40	0	omnivore	0	1	cavity	0	1.78
Melanerpes formicivorus	79.00	0	seed	1	0	cavity	0	1.99
Melanerpes lewis	103.90	0	omnivore	1	1		0	2.22
Melanitta deglandi	1545.60	0	invertebrate		1		0	6.68
Melanitta perspicillata	992.30	0	invertebrate	1	1		0	5.70
Meleagris gallopavo	6572.88	0	omnivore	1	0	open	0	7.17
Melospiza georgiana	17.85	0	omnivore	1	1		1	0.81
Melospiza melodia	20.85	0	seed	1	1		1	0.94
Micrathene whitneyi	35.00	0	invertebrate		1	cavity	0	1.40
Mimus polyglottos	45.20	1	omnivore		1	open	0	1.38
Mniotilta varia	12.00	0	invertebrate	1	1	open	1	0.44
Morus bassanus	2999.50	0	vertfishscav	1	0	open	0	18.53
Motacilla alba	21.78	0	invertebrate	1	1	cave	0	0.60

Species	Body Mass	Vocal Mimicry	Diet	Sociality	Migration	Nest Type	Parasitised	Brain Volume
Myadestes townsendi	32.50	0	invertebrate	0	1		1	1.01
Mycteria americana	2505.00	0	vertfishscav	1	1	open	0	14.88
Myiarchus cinerascens	28.80	0	invertebrate	1	1		0	0.77
Myiarchus tuberculifer	18.70	0	invertebrate	1	0		0	0.66
Myiarchus tyrannulus	35.30	0	invertebrate		1		1	0.98
Myioborus pictus	9.80	0	invertebrate	1	1		1	0.39
Myiopsitta monachus	120.00		seed		0	closed	0	3.89
Myiozetetes similis	27.80	0	invertebrate	1	1		0	0.82
Numenius americanus	510.20		invertebrate	1	1	open	0	3.80
Numenius phaeopus	381.25		invertebrate	0	1	open	0	3.13
Nyctanassa violacea	682.50	0	invertebrate	0	1		0	5.98
Nycticorax nycticorax	756.05	0	vertfishscav	0	1	open	0	6.66
Nyctidromus albicollis	54.80	0	invertebrate		0	open	0	0.91
Oceanodroma leucorhoa	44.95	0	vertfishscav	1	0	cavity	0	0.89
Pandion haliaetus	1504.33	0	vertfishscav	1	1		0	9.38
Parabuteo unicinctus	863.20	0	vertfishscav	1	0	open	0	7.98
Parula americana	8.00	0	invertebrate	1	1	open	1	0.39
Parus atricapillus	11.41	0	invertebrate	1	0	cavity	0	0.76
Parus carolinensis	10.20	0	invertebrate	1	0	cavity	0	0.60
Parus gambeli	11.30	0	invertebrate	1	0	cavity	0	0.69
Parus hudsonicus	11.00	0	invertebrate	1	0		0	0.71
Passer montanus	21.74	0	seed	1	0	cavity	0	0.75

Species	Body Mass	Vocal Mimicry	Diet	Sociality	Migration	Nest Type	Parasitised	Brain Volume
Passerculus sandwichensis	20.10	0	invertebrate	1	1		1	0.68
Passerina cyanea	12.20	0	seed	1	1	open	1	0.65
Patagioenas fasciata	353.10	0	seed	1	1	open	0	2.12
Pelecanus erythrorhynchos	6324.75	0	vertfishscav	1	1	open	0	24.25
Perisoreus canadensis	69.00	1	omnivore	1	0		0	2.53
Petrochelidon fulva	15.50	0	invertebrate	1	1		0	0.50
Phainopepla nitens	22.40	1	fruit	0	1	open	0	0.79
Phalacrocorax auritus	1531.00	0	vertfishscav	1	1	open	0	7.32
Phalacrocorax carbo	2405.83	0	vertfishscav	1	1	open	0	10.45
Phalaenoptilus nuttallii	51.60	0	invertebrate		1	open	0	0.53
Phalaropus lobatus	35.30		invertebrate	1	1	open	0	0.45
Pheucticus ludovicianus	44.40	1	fruit	1	1	open	1	1.32
Philomachus pugnax	158.67		invertebrate	1	1	open	0	1.56
Phoebastria nigripes	3148.00	0	vertfishscav		1	open	0	15.80
Picoides arcticus	72.40	0	invertebrate	1	0		0	3.15
Picoides borealis	47.90	0	invertebrate	1	0		0	1.66
Picoides pubescens	25.30	0	invertebrate	1	0		0	1.21
Picoides tridactylus	55.20	0	invertebrate	0	0	cavity	0	2.63
Picoides villosus	73.30	0	invertebrate	0	0		0	2.95
Pinicola enucleator	65.70	1	seed	1	1	open	0	1.58
Pipilo aberti	39.20	0	invertebrate		0		1	1.36
Pipilo erythrophthalmus	39.20	0	seed	1	1	open	1	1.36

Species	Body Mass	Vocal Mimicry	Diet	Sociality	Migration	Nest Type	Parasitised	Brain Volume
Pipilo fuscus	39.20	0	seed		0	open	1	1.36
Piranga ludoviciana	30.00	0	invertebrate	0	1		0	0.98
Piranga rubra	29.50	0	invertebrate	0	1		0	1.02
Pitangus sulphuratus	70.85	0	omnivore	1	1	closed	1	1.35
Plegadis chihi	612.50	0	invertebrate	1	0		0	5.04
Plegadis falcinellus	623.33	0	invertebrate	1	1	open	0	5.12
Podiceps auritus	445.60	0	vertfishscav	1	1	open	0	2.43
Podiceps grisegena	972.23	0	invertebrate	1	1	open	0	4.04
Polioptila caerulea	6.00	1	invertebrate	1	1		1	0.30
Pooecetes gramineus	25.70	0	seed	0	1	open	1	0.81
Porphyrio martinica	218.30	0	vegetation	0	1		0	2.47
Porzana carolina	80.80	0	omnivore	0	1	open	0	1.16
Protonotaria citrea	15.50	0	invertebrate	1	1	cavity	1	0.59
Psaltriparus minimus	5.30	0	invertebrate	1	0		0	0.35
Psittacula krameri	137.00		fruit		0		0	4.07
Ptychoramphus aleuticus	191.80		invertebrate	1	1	cavity	0	2.06
Puffinus griseus	770.00	0	vertfishscav	1	1	cavity	0	5.31
Puffinus puffinus	453.00	0	vertfishscav	1	1	cavity	0	3.43
Puffinus tenuirostris	534.47	0	vertfishscav	1	1	cavity	0	4.64
Pyrocephalus rubinus	12.70	0	invertebrate		1	open	1	0.46
Quiscalus major	158.80	0	omnivore	1	0	open	0	2.78
Quiscalus mexicanus	168.70	0	omnivore	1	0	open	1	2.96

Species	Body Mass	Vocal Mimicry	Diet	Sociality	Migration	Nest Type	Parasitised	Brain Volume
Quiscalus quiscula	98.00	0	omnivore	1	1	open	1	2.59
Recurvirostra americana	325.70	0	invertebrate	1	1	open	0	2.10
Regulus calendula	6.95	0	invertebrate	1	1		1	0.31
Regulus satrapa	6.20	0	invertebrate	1	1		0	0.36
Rissa tridactyla	446.70	0	invertebrate	1	1	open	0	4.31
Rostrhamus sociabilis	420.00	0	invertebrate		1	open	1	5.09
Rynchops niger	307.10		vertfishscav	1	1	open	0	2.64
Salpinctes obsoletus	16.00	0	invertebrate		1	cavity	0	0.75
Sayornis phoebe	18.30	0	invertebrate	1	1	open	1	0.59
Sayornis saya	21.70	0	invertebrate	0	1	cave	0	0.61
Scolopax minor	197.50		invertebrate	1	1	open	0	2.02
Seiurus aurocapilla	19.50	0	invertebrate	0	1	open	1	0.70
Selasphorus rufus	3.45	0	nectar	0	1		0	0.14
Setophaga ruticilla	7.50	0	invertebrate	0	1	open	1	0.36
Sialia mexicana	26.40	0	invertebrate	1	1	cavity	1	0.84
Sialia sialis	29.70	0	invertebrate	1	1	cavity	1	0.99
Sitta canadensis	11.00	0	seed	1	1	cavity	0	0.57
Sitta carolinensis	17.80	0	seed	1	0	cavity	0	0.86
Sitta pygmaea	10.40	0	seed	1	0	cavity	0	0.55
Sphyrapicus nuchalis	45.60	0	invertebrate	0	1		0	1.27
Sphyrapicus varius	49.90	0	invertebrate	0	1		0	1.30
Spiza americana	27.00	0	seed		1	open	1	0.91

Species	Body Mass	Vocal Mimicry	Diet	Sociality	Migration	Nest Type	Parasitised	Brain Volume
Spizella arborea	12.40	0	invertebrate	1	1		0	0.74
Steganopus tricolor	61.00		invertebrate		1		0	0.65
Stercorarius parasiticus	470.30		vertfishscav		1	open	0	3.89
Sterna fuscata	185.50		omnivore		1	open	0	2.32
Sterna hirundo	113.67		vertfishscav	1	1	open	0	1.74
Sterna paradisaea	112.25		vertfishscav	1	1	open	0	2.00
Sterna sandvicensis	250.00		vertfishscav	1	1		0	2.70
Streptopelia roseogrisea	143.50		fruit	1	1		0	1.10
Strix nebulosa	1067.45	0	vertfishscav		1	open	0	14.66
Strix varia	717.05	0	vertfishscav		0	cavity	0	12.55
Strix virgata	279.50	0	invertebrate		0		0	6.10
Sturnella magna	89.00	0	invertebrate	1	0	open	1	2.22
Sturnella neglecta	103.50	0	invertebrate	1	1	open	1	1.94
Sula nebouxii	1237.50	0	vertfishscav	1	0	open	0	9.04
Surnia ulula	303.45	0	vertfishscav		1	cavity	0	7.48
Tachycineta bicolor	20.10	0	invertebrate	1	1		0	0.55
Tachycineta thalassina	15.10	0	invertebrate	1	1	cavity	0	0.46
Thryomanes bewickii	9.80	0	invertebrate	1	1	cavity	0	0.52
Thryothorus ludovicianus	18.70	0	invertebrate	1	0	cavity	1	0.85
Tiaris olivaceus	8.50	0	seed	1	0	closed	0	0.48
Toxostoma curvirostre	78.40	1	omnivore		0		0	2.13
Toxostoma rufum	70.30	1	omnivore	1	1	open	0	2.00

Species	Body Mass	Vocal Mimicry	Diet	Sociality	Migration	Nest Type	Parasitised	Brain Volume
Tringa erythropus	151.50		invertebrate	1	1	open	0	1.74
Tringa flavipes	82.40		invertebrate	1	1	open	0	1.07
Tringa glareola	67.50		invertebrate	0	1	open	0	1.04
Tringa nebularia	163.01		invertebrate	1	1	open	0	1.66
Troglodytes aedon	10.56	0	invertebrate	0	1	cavity	0	0.53
Troglodytes troglodytes	9.39	0	invertebrate	0	1	closed	1	0.49
Turdus migratorius	79.60	0	fruit	1	1	open	1	1.64
Tympanuchus phasianellus	847.80	0	vegetation		0	open	0	2.88
Tyrannus dominicensis	46.30	0	invertebrate		0		1	1.00
Tyrannus forficatus	39.30	0	invertebrate	1	1		1	0.86
Tyrannus savana	28.60	0	invertebrate	1	1		1	0.73
Tyrannus tyrannus	39.70	0	invertebrate	1	1		1	0.95
Tyrannus verticalis	40.70	0	invertebrate	1	1		1	0.98
Tyto alba	358.22	0	vertfishscav	0	0	cavity	0	6.41
Uria aalge	918.60		vertfishscav	1	1	open	0	5.73
Uria lomvia	967.35		vertfishscav	1	1	open	0	5.30
Vermivora peregrina	9.50	0	invertebrate	1	1	open	1	0.43
Vermivora pinus	8.40	0	invertebrate	1	1	open	1	0.41
Vireo altiloquus	19.50	0	invertebrate		1		1	0.75
Vireo griseus	11.90	1	invertebrate	1	1	open	1	0.58
Vireo olivaceus	20.30	0	invertebrate	1	1	open	1	0.61
Vireo philadelphicus	12.20	1	invertebrate	1	1		1	0.46

Species	Body Mass	Vocal Mimicry	Diet	Sociality	Migration	Nest Type	Parasitised	Brain Volume
Volatinia jacarina	12.50	0	seed	1	0		0	0.49
Wilsonia citrina	10.70	0	invertebrate	0	1		1	0.48
Xanthocephalus xantho-cephalus	76.60	0	seed	1	1		1	1.65
Zenaida macroura	126.50	0	seed	1	1	open	0	1.19
Zonotrichia albicollis	25.80	0	seed	1	1	open	1	1.05
Zonotrichia leucophrys	25.55	0	seed	1	1	open	1	0.97

1.6 Carnivore Data

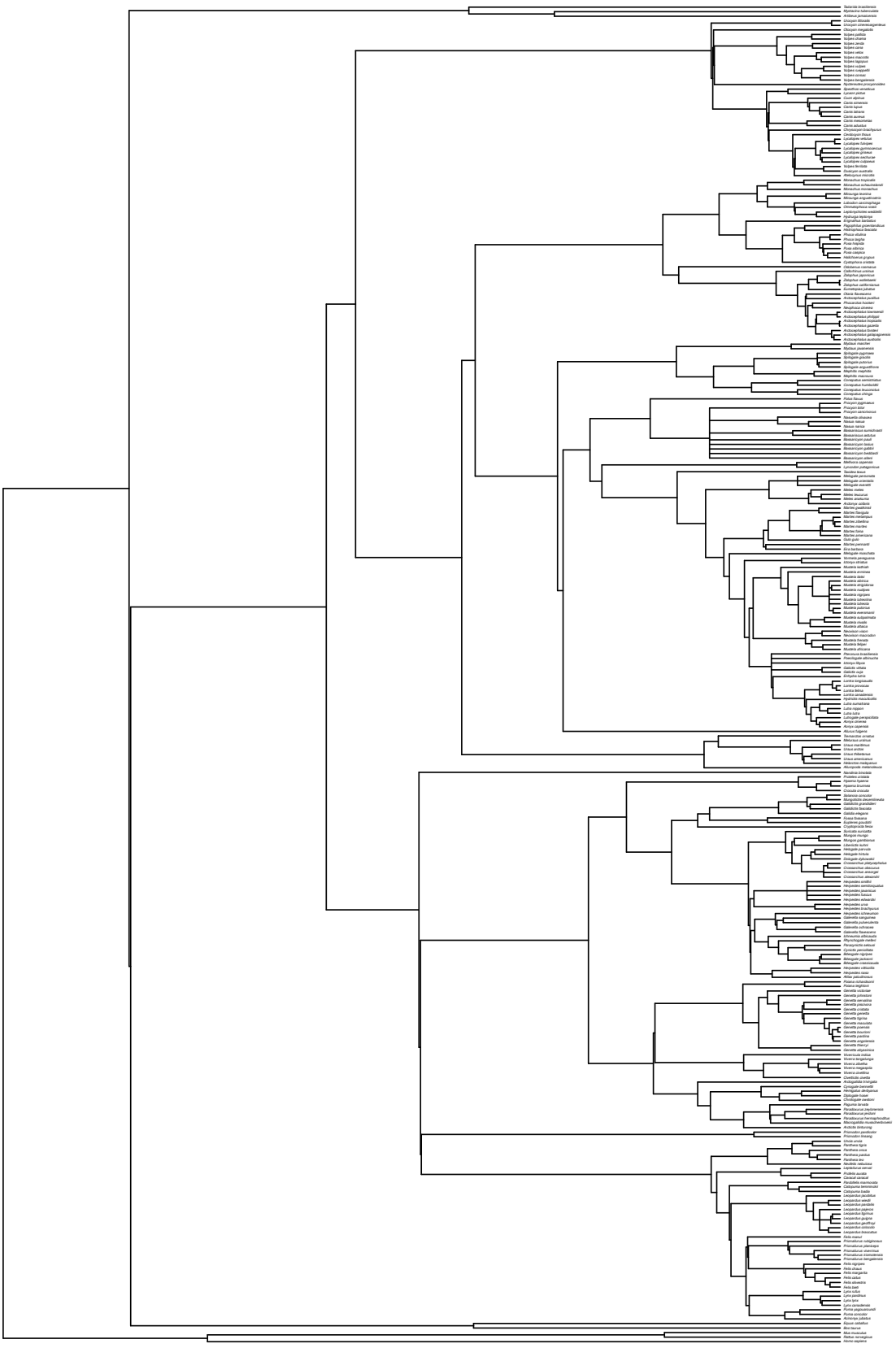

Figure 1.8: Phylogeny of carnivores (Nyakatura and Bininda-Emonds 2012).

Table 1.16: Phenotypic data on body size, brain size, group size, diet breadth, gestation, inter-birth interval, litter size, longevity, age at sexual maturity and age at weaning in carnivores.

Species	Family	Body Mass	Brain Volume	Group Size	Diet Breadth	Gestation Period	Inter-birth Interval	Litter Size	Longevity	Age at Sexual Maturity	Age at Weaning
Acinonyx jubatus	Felidae	50.00	111.05	1.00	1	92.24	547.50	3.28	228.00	741.97	91.42
Ailuropoda melanoleuca	Ursidae	108.40	235.10	1.00	3	134.99	638.75	1.62	360.00	2413.02	178.98
Ailurus fulgens	Ailuridae	4.90	40.85		3	131.50	365.00	1.70	168.00	604.05	136.87
Aonyx capensis	Mustelidae	19.00	94.63		6	62.99		2.62	132.00	371.23	
Aonyx cinerea	Mustelidae	1.75	38.08	11.00	2	63.31	182.50	1.47	121.00		79.54
Arctictis binturong	Viverridae	9.88	40.85	1.00	3	92.24	317.60	2.50	272.40	1034.61	117.57
Arctocephalus australis	Otariidae				6	246.38	365.00	1.00	252.00	1729.33	365.00
Arctocephalus forsteri	Otariidae				6	242.47	365.00	1.00	180.00	2668.42	323.72
Arctocephalus galapagoensis	Otariidae				6	215.94	730.00	1.00	264.00	1683.65	821.25
Arctocephalus gazella	Otariidae				1	294.69	365.00	1.00	276.00	1691.66	116.28
Arctocephalus philippii	Otariidae				6		365.00	1.00			
Arctocephalus pusillus	Otariidae				1	357.99	365.00	1.00	252.00	1698.17	356.30
Arctocephalus townsendi	Otariidae				1		365.00	1.00	288.00		328.13
Arctocephalus tropicalis	Otariidae				6	241.69	365.00	1.40	276.00	1538.68	304.16
Arctogalidia trivirgata	Viverridae	2.25	21.98	1.00	6	45.95	182.50	2.79	190.00	841.82	49.41
Arctonyx collaris	Mustelidae	6.36	49.40	1.00	6	42.89		3.00	167.00		165.64
Atelocynus microtis	Canidae	7.75	62.18	1.00	1				132.00		
Atilax paludinosus	Herpestidae	3.30	28.50	1.00	6	77.27	182.50	2.00	209.00	234.83	35.89

Species	Family	Body Mass	Brain Volume	Group Size	Diet Breadth	Gestation Period	Inter-birth Interval	Litter Size	Longevity	Age at Sexual Maturity	Age at Weaning
Bassaricyon alleni	Procyonidae	1.24	18.48								
Bassaricyon gabbii	Procyonidae	1.25	17.02		6	76.65		1.00	300.00	607.20	89.49
Bassariscus astutus	Procyonidae	1.13	16.44	1.00	6	54.23	365.00	3.00	198.00	278.08	53.84
Bassariscus sumichrasti	Procyonidae	0.90	19.30	1.00	6			2.00	276.00	841.82	119.32
Bdeogale crassicauda	Herpestidae	1.55	16.95	1.00	1			0.96			
Bdeogale jacksoni	Herpestidae				2						
Bdeogale nigripes	Herpestidae			1.00	6			1.00	190.00		
Callorhinus ursinus	Otariidae				6	358.49	365.00	1.04	420.00	1683.65	108.69
Canis adustus	Canidae	10.25	51.94	2.00	6	65.00		4.50	137.00	249.88	52.89
Canis aureus	Canidae	10.35	72.24	3.30	6	61.24	365.00	3.74	192.00	371.23	61.30
Canis latrans	Canidae	13.41	88.23	2.10	1	61.74	365.00	5.72	262.00	372.90	43.71
Canis lupus	Canidae	29.00	131.60	7.00	1	63.50	365.00	4.98	354.00	679.37	44.82
Canis mesomelas	Canidae	8.50	51.42	2.00	6	62.50	273.75	3.89	168.00	241.40	34.10
Canis simensis	Canidae	10.00	80.67	8.00	1	63.61	365.00			754.74	69.60
Caracal caracal	Felidae	13.75	55.15	1.00	1	71.47	365.00	2.30	204.00	437.27	120.41
Catopuma temminckii	Felidae	11.50	68.03		1	99.07		1.50	216.00		
Chrotogale owstoni	Viverridae				6						
Chrysocyon brachyurus	Canidae	23.25	120.30	1.00	6	63.48		2.00	180.00	420.91	119.00
Civettictis civetta	Viverridae	12.00	36.97	1.00	6	68.40	212.14	2.31	336.00	286.24	82.91
Conepatus chinga	Mephitidae	1.92	14.78	1.00							
Conepatus humboldtii	Mephitidae	1.32	12.57	1.00	1			3.49			

Species	Family	Body Mass	Brain Volume	Group Size	Diet Breadth	Gestation Period	Inter-birth Interval	Litter Size	Longevity	Age at Sexual Maturity	Age at Weaning
Conepatus leuconotus	Mephitidae	3.50	14.44	1.00	1	60.83	182.50	3.60	84.00	340.60	45.56
Conepatus mesoleucus	Mephitidae	2.01	15.50								
Conepatus semistriatus	Mephitidae	2.04	18.92	1.00	6			3.49			
Crocuta crocuta	Hyaenidae	63.00	144.03	55.00	1	112.33	441.04	1.91	493.20	789.54	371.37
Crossarchus alexandri	Herpestidae							4.00			
Crossarchus ansorgei	Herpestidae				6						
Crossarchus obscurus	Herpestidae	1.25	9.78	20.00	6	70.00	121.66	4.29	108.00	278.42	29.23
Cryptoprocta ferox	Eupleridae	9.50	32.14	1.00	2	92.54		2.98	240.00	1262.74	136.10
Cuon alpinus	Canidae	12.76	95.00	6.30	1	61.50	365.00	4.30	192.00	374.18	57.33
Cynictis penicillata	Herpestidae	0.84	10.49	3.50	1	56.83	365.00	2.15	182.40	350.57	41.76
Cynogale bennettii	Viverridae	4.50	29.96	1.00	6			2.30	60.00		
Cystophora cristata	Phocidae				6	334.58	365.00	1.00	420.00	1262.74	9.50
Diplogale hosei	Viverridae				6						
Dologale dybowskii	Herpestidae							4.00			
Dusicyon australis	Canidae				1						
Cerdocyon thous	Canidae	5.24	41.80	2.00	7	57.18	243.33	3.09	138.00	279.15	72.33
Eira barbara	Mustelidae	3.91	35.87	1.00	2	66.74		2.14	216.00	766.15	94.46
Enhydra lutris	Mustelidae	23.50	125.21	1.00	6	238.00	365.00	0.96	360.00	1022.33	178.98
Erignathus barbatus	Phocidae				6	285.24	547.50	1.00	377.43	2199.16	20.94
Eumetopias jubatus	Otariidae				6	342.10	365.00	0.96	360.00	1965.83	351.00
Eupleres goudotii	Eupleridae	3.00	16.95	1.00	6	93.86		1.00			62.99

Species	Family	Body Mass	Brain Volume	Group Size	Diet Breadth	Gestation Period	Inter-birth Interval	Litter Size	Longevity	Age at Sexual Maturity	Age at Weaning
Felis catus	Felidae					62.99			408.00	296.98	
Felis chaus	Felidae	7.39	39.25		1	62.88	130.01	2.94	144.00	383.18	95.49
Felis margarita	Felidae				1	63.61	197.70	4.12			
Felis nigripes	Felidae	1.30	20.09	1.00	1	67.50	228.12	1.78	144.00	284.58	67.23
Felis silvestris	Felidae	5.53	37.34	1.00	1	65.49	148.25	3.59	336.00	350.76	76.01
Fossa fossana	Eupleridae	1.50	19.69	2.00	6	88.38	365.00	1.00	132.00	533.97	66.84
Galerella pulverulenta	Herpestidae	0.80	11.02	1.00	2			2.25	104.50		
Galerella sanguinea	Herpestidae	0.55	8.76	1.30	6	61.27	182.50	2.50	72.00	465.57	54.44
Galictis cuja	Mustelidae	1.00	15.03	1.00	1				87.00		
Galictis vittata	Mustelidae	3.20	24.30	1.00							
Galidia elegans	Eupleridae	0.80	10.70	3.00	6	76.11	365.00	1.00	158.40	742.46	59.27
Galidictis fasciata	Eupleridae				2		365.00	1.00			
Galidictis grandidieri	Eupleridae				2		365.00	1.00			
Genetta angolensis	Viverridae	1.65	15.49								
Genetta cristata	Viverridae				2			2.50	408.00		
Genetta genetta	Viverridae	2.00	14.01	1.00	6	74.18	182.50	2.29	408.00	1262.74	71.80
Genetta maculata	Viverridae				6			2.12			
Genetta piscivora	Viverridae				1			0.96			
Genetta servalina	Viverridae	1.06	15.03	1.00	6			1.50			
Genetta tigrina	Viverridae	2.23	15.18	1.00	6	71.48	304.16	2.76	180.00	841.82	87.77
Gulo gulo	Mustelidae	17.01	78.26	1.00	1	161.73	821.25	2.84	216.00	756.60	83.64

Species	Family	Body Mass	Brain Volume	Group Size	Diet Breadth	Gestation Period	Inter-birth Interval	Litter Size	Longevity	Age at Sexual Maturity	Age at Weaning
Halichoerus grypus	Phocidae				2	349.79	365.00	0.96	560.07	1770.72	18.37
Helarctos malayanus	Ursidae	46.50	345.25	1.00	3	98.34		1.10	297.60		90.36
Helogale hirtula	Herpestidae				1						
Helogale parvula	Herpestidae	0.30	4.76	9.50	1	54.08	141.94	3.49	131.00	423.04	21.00
Hemigalus derbyanus	Viverridae	2.12	18.92		6			1.73	144.00		69.60
Puma yagouaroundi	Felidae	7.87	40.04	1.00	3	75.01	182.50	2.50	127.83	1052.28	
Herpestes brachyurus	Herpestidae				1			3.49			
Herpestes edwardsi	Herpestidae	1.32	10.49	1.00	6	63.09	109.50	2.00		311.36	34.80
Herpestes ichneumon	Herpestidae	5.18	23.34		6	75.87	365.00	3.00	240.00	729.99	58.09
Herpestes javanicus	Herpestidae	0.74	7.24	1.00	6	48.48	152.08	2.21	120.00	166.84	43.59
Herpestes naso	Herpestidae	3.00	25.53	1.00	1						
Herpestes smithii	Herpestidae	1.78	13.74	1.00	6			2.50			
Herpestes urva	Herpestidae	1.86	20.91	1.00	6	65.70		3.00	160.00		
Herpestes vitticollis	Herpestidae	2.58	25.79	1.00				2.73			
Hyaena hyaena	Hyaenidae	41.71	97.51	1.00	6	90.50	237.25	2.44	288.00	928.08	118.93
Hydrictis maculicollis	Mustelidae	4.00	40.04	5.00	1	59.60	365.00	2.00		841.82	60.48
Hydrurga leptonyx	Phocidae				6	272.79	365.00	0.96	312.00	1389.01	30.41
Ichneumia albicauda	Herpestidae	3.50	24.29	1.00	1			2.35	144.00	754.74	
Ictonyx libyca	Mustelidae	0.63	4.48	1.00	6	37.78		2.00	60.00		
Ictonyx striatus	Mustelidae	1.30	9.78	1.00	6	36.76	365.00	2.30	160.00	447.70	59.09
Leopardus geoffroyi	Felidae	3.59	34.00	1.00							

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Leopardus guigna	Felidae	2.03	28.34								
Leopardus jacobitus	Felidae				1						
Leopardus pardalis	Felidae	11.90	63.43	1.00	1	81.99	360.90	1.66	243.60	678.64	106.18
Leopardus wiedii	Felidae	3.65	44.83	1.00	1	82.20		1.50	240.00	1052.28	93.40
Leptailurus serval	Felidae	12.00	56.80	1.00	1	73.74	182.50	2.35	276.00	887.95	104.68
Leptonychotes weddellii	Phocidae				6	314.99	365.00	1.00	300.00	1587.55	43.35
Liberiictis kuhni	Herpestidae				6						
Lobodon carcinophaga	Phocidae				1	269.81	547.50	0.96	468.00	1522.50	31.32
Lontra canadensis	Mustelidae	8.09	52.98	15.00	1	58.40	365.00	2.67	300.00	729.99	121.66
Lontra felina	Mustelidae	4.50	38.86	1.00	2	75.97	365.00	2.54			
Lontra longicaudis	Mustelidae	8.00	57.40	1.00	2			3.69			
Lontra provocax	Mustelidae				2						
Lutra lutra	Mustelidae	8.79	42.10	1.00	1	64.27	365.00	2.01	264.00	700.76	100.80
Lutra sumatrana	Mustelidae				1						
Lutrogale perspicillata	Mustelidae	9.00	64.72	2.00	2	63.31		3.24	180.00	943.94	72.53
Lycalopex culpaeus	Canidae	9.83	51.50	1.00	2	58.72	365.00	4.88		377.37	48.22
Lycalopex fulvipes	Canidae		34.41	1.00							
Lycalopex griseus	Canidae		41.76	2.00							
Lycalopex gymnocercus	Canidae	4.69	40.00	1.00	7	59.23	365.00	3.09	164.40		
Lycalopex sechurae	Canidae		34.66		7						
Lycalopex vetulus	Canidae		37.77		6		365.00	3.00			

Species	Family	Body Mass	Brain Volume	Group Size	Diet Breadth	Gestation Period	Inter-birth Interval	Litter Size	Longevity	Age at Sexual Maturity	Age at Weaning
Lycaon pictus	Canidae	22.05	129.00	8.00	1	71.18	355.87	8.10	132.00	817.15	27.28
Lynx canadensis	Felidae	7.32	52.98	1.00	1	62.50	365.00	2.73	321.00	672.90	111.36
Lynx lynx	Felidae	17.95	70.11	1.00	1	66.99	365.00	2.30	321.60	739.52	81.85
Lynx pardinus	Felidae				1	69.44		2.50			
Lynx rufus	Felidae	8.90	57.97	1.00	1	59.99	365.00	2.76	388.00	668.22	59.99
Macrogalidia musschenbroekii	Viverridae				6						
Martes americana	Mustelidae	1.25	15.80	1.00	1	27.63	365.00	2.60	228.00	456.25	45.73
Martes flavigula	Mustelidae	1.84	34.12	2.00	1	149.65	182.50	3.53	168.00	1262.74	89.49
Martes foina	Mustelidae	1.54	20.91	1.00	1	29.86	365.00	3.78	217.20	742.46	74.11
Martes gwatkinsii	Mustelidae				3						90.73
Martes martes	Mustelidae	1.30	20.00	1.50	1	30.63	365.00	3.49	204.00	508.47	54.19
Martes pennanti	Mustelidae	4.00	31.82	1.00	1	31.28	365.00	3.02	121.76	413.84	76.76
Martes zibellina	Mustelidae	1.13	18.50	1.00	6	30.80		3.13	180.00	479.51	52.23
Meles meles	Mustelidae	13.00	50.40	7.00	1	48.60	365.00	3.11	194.40	420.91	91.30
Mellivora capensis	Mustelidae	8.50	72.97	1.00	6	181.46	182.50	2.35	318.00		23.86
Melogale everetti	Mustelidae				6			2.00			
Melogale moschata	Mustelidae	0.81	15.07	1.00	6			2.00	126.00		
Melogale personata	Mustelidae	1.70	13.83	1.00	6			2.50			
Melursus ursinus	Ursidae	93.13	304.90	1.00	6	203.36	1095.00	1.54	480.00	1262.74	194.67
Mephitis macroura	Mephitidae	1.03	10.07		1	58.20		4.68			
Mephitis mephitis	Mephitidae	2.09	10.28	1.00	6	63.29	365.00	5.70	155.00	355.18	55.15

Species	Family	Body Mass	Brain Volume	Group Size	Diet Breadth	Gestation Period	Inter-birth Interval	Litter Size	Longevity	Age at Sexual Maturity	Age at Weaning
Mirounga angustirostris	Phocidae				6	290.63	365.00	1.00	243.50	1522.50	27.37
Mirounga leonina	Phocidae				2	243.33	365.00	1.00	276.00	1607.08	22.93
Monachus monachus	Phocidae				6	334.58	730.00	1.00	284.40	1567.84	42.75
Monachus schauinslandi	Phocidae				6	344.15	467.39	1.00	360.00	1687.65	37.13
Monachus tropicalis	Phocidae				1		547.50	1.00			
Mungos gambianus	Herpestidae				6						
Mungos mungo	Herpestidae	1.93	10.49	16.30	1	60.91	365.00	2.68	144.00	349.33	20.88
Mungotictis decemlineata	Eupleridae				2	100.83		0.99		755.15	45.10
Mustela altaica	Mustelidae	0.17	4.50		1	40.00	365.00	5.44			56.00
Mustela erminea	Mustelidae	0.12	4.00	1.00	1	66.35	365.00	6.74	85.23	93.09	60.93
Mustela eversmanii	Mustelidae				1	40.14	365.00	7.82		326.63	48.80
Mustela frenata	Mustelidae	0.15	4.01	1.00	1	24.50	365.00	6.50	85.23	200.69	34.23
Mustela kathiah	Mustelidae	0.21	4.41		1						
Mustela lutreola	Mustelidae	0.44	8.50		2	43.74	365.00	4.50	120.00	351.71	58.71
Mustela lutreolina	Mustelidae	5.38	8.50		1						
Mustela nigripes	Mustelidae	0.85	8.50	1.00	1	43.00	365.00	3.36	144.00	371.23	59.66
Mustela nivalis	Mustelidae	0.10	1.99	1.00	1	36.49	273.75	5.07	120.00	169.99	36.74
Mustela nudipes	Mustelidae							4.00			
Mustela putorius	Mustelidae	0.92	8.30	1.00	1	41.49	252.50	8.48	168.00	308.50	54.39
Mustela sibirica	Mustelidae	0.41	6.75	1.00	1	30.12		6.48	106.00		58.20
Mydaus javanensis	Mephitidae	2.50	19.49		6						

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Nandinia binotata	Nandiniidae	2.00	17.29	1.00	2	65.35	182.50	1.84	222.00	1015.00	63.81
Nasua narica	Procyonidae	3.87	29.96	1.60	6	76.82	365.00	4.00	212.00	1009.04	132.63
Nasua nasua	Procyonidae	3.00	30.00	20.00	6	75.06	365.00	3.69	212.40	841.82	113.15
Nasuella olivacea	Procyonidae				6						
Neofelis nebulosa	Felidae	19.68	68.71		1	93.44		2.25	204.00	753.48	111.67
Neophoca cinerea	Otariidae				6	265.94	539.89	1.35	192.00	1587.55	542.19
Neovison vison	Mustelidae	0.95	8.50	1.00							
Nyctereutes procyonoides	Canidae	4.04	28.50	2.00	6	61.84	365.00	6.36	168.00	326.63	49.69
Odobenus rosmarus	Odobenidae				6	357.39	821.25	1.22	480.00	2315.02	591.36
Ommatophoca rossii	Phocidae				1	349.79	365.00	0.96	252.00	1489.84	27.84
Otaria flavescens	Otariidae					311.55	365.00	1.00	297.60	1860.83	363.96
Felis manul	Felidae	3.50	34.47		1	76.08		4.83			
Otocyon megalotis	Canidae	4.15	26.84	2.00	1	67.54	182.50	4.00	165.60	420.91	42.46
Paguma larvata	Viverridae	4.30	30.88	1.00	6		182.50	2.16	216.00		109.13
Panthera leo	Felidae	161.50	223.63	8.70	1	108.74	730.00	2.75	360.00	987.77	197.86
Panthera onca	Felidae	100.00	151.41		1	102.49	365.00	1.96	276.00	1184.16	156.60
Panthera pardus	Felidae	52.04	125.21	1.00	1	96.74	476.37	2.14	276.00	810.68	123.54
Panthera tigris	Felidae	162.56	278.66	1.00	1	105.19	821.25	2.60	315.60	1522.50	118.55
Paracynictis selousi	Herpestidae	1.64	15.80	1.00	1			2.00			
Paradoxurus hermaphroditus	Viverridae	3.16	18.50	1.00	6	61.27	182.50	3.29	269.00	397.85	
Paradoxurus jerdoni	Viverridae				6			3.00	144.00		

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Paradoxurus zeylonensis	Viverridae	2.78	17.81	1.00	6			2.50			
Hyaena brunnea	Hyaenidae	32.20	106.70	9.00	6	95.80	532.29	2.30	204.00	807.23	302.44
Pardofelis marmorata	Felidae				1			2.00			
Histriophoca fasciata	Phocidae				6	299.18	365.00	1.00	372.00	1262.74	24.50
Pagophilus groenlandicus	Phocidae				6	242.90	365.00	1.00	504.00	1862.30	11.45
Phoca largha	Phocidae				6	287.40	365.00	1.00	426.13	1497.64	27.84
Phoca vitulina	Phocidae				1	288.95	365.00	1.00	480.00	1526.85	30.74
Phocarctos hookeri	Otariidae				7	365.00	365.00	1.00		2030.00	252.01
Poecilogale albinucha	Mustelidae	0.34	4.76	1.00	1	32.55	243.33	2.23	62.40	914.79	76.56
Poiana richardsonii	Viverridae				6			2.23	64.00		
Potos flavus	Procyonidae	3.00	25.53	1.00	4	116.80	365.00	1.11	348.00	858.41	109.13
Prionailurus bengalensis	Felidae	3.30	29.37	1.00	1	70.18	165.56	2.50	180.00	855.31	24.85
Prionailurus planiceps	Felidae				2	56.00					
Prionailurus rubiginosus	Felidae	2.77	18.92		1			2.23			
Prionailurus viverrinus	Felidae	9.14	46.53		1	71.43		2.00	120.00		135.96
Prionodon linsang	Viverridae	0.70	8.50	1.00	6		182.50	2.30	128.40		
Prionodon pardicolor	Viverridae	0.51	9.03	1.00	6		182.50	2.00			
Procyon cancrivorus	Procyonidae	6.95	59.45	1.00	6	69.35		2.62	168.00	631.37	111.36
Procyon lotor	Procyonidae	5.53	40.04	1.00	6	65.00	365.00	3.06	252.00	561.28	104.16
Procyon pygmaeus	Procyonidae				3						
Profelis aurata	Felidae	10.65	57.97		1	81.34		2.25		650.61	119.32

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Proteles cristata	Hyaenidae	10.00	35.16	1.30	1	90.62		2.64	300.00	631.37	125.73
Pteronura brasiliensis	Mustelidae	24.00	85.63	6.00	1	70.00	365.00	2.12	154.00		120.48
Puma concolor	Felidae	51.60	125.21	1.00	1	92.30	577.91	2.76	240.00	1034.61	48.46
Pusa caspica	Phocidae				2	334.58	365.00	1.00	600.00	2199.16	31.32
Pusa hispida	Phocidae				6	270.00	365.00	1.00	552.00	2251.64	45.23
Pusa sibirica	Phocidae				1	277.63	365.00	1.00	672.00	2276.14	66.11
Rhynchogale melleri	Herpestidae	2.50	16.95	1.00	6			2.00			
Salanoia concolor	Eupleridae	0.65	11.02		3				57.60		
Speothos venaticus	Canidae	6.00	40.45	4.00	1	67.78	247.94	3.80	124.00	344.87	127.30
Spilogale putorius	Mephitidae	0.34	5.00	1.00	6	32.99	243.33	5.07	120.00	196.96	55.68
Spilogale pygmaea	Mephitidae				6	47.22		4.00			
Suricata suricatta	Herpestidae	0.73	10.28	6.35	1	77.00	365.00	3.86	150.00	377.37	55.68
Taxidea taxus	Mustelidae	7.11	48.91	1.00	1	43.80	365.00	2.76	312.00	365.00	41.99
Tremarctos ornatus	Ursidae	110.00	195.27	1.00	5	215.00		1.44	437.00		173.44
Uncia uncia	Felidae	44.17	101.49	1.00	1	100.95	365.00	2.12	216.00	841.82	101.42
Urocyon cinereoargenteus	Canidae	3.83	40.85	1.00	6	61.48	365.00	3.71	180.00	350.76	63.79
Urocyon littoralis	Canidae	1.90	27.66	2.00	6	53.70	365.00	2.17	96.00	361.52	
Ursus americanus	Ursidae	99.95	259.82	1.00	1	213.95	821.25	2.39	384.00	1448.45	167.99
Ursus arctos	Ursidae	172.72	338.30	1.00	6	227.56	912.50	2.24	600.00	1327.95	182.50
Ursus maritimus	Ursidae	388.75	459.44	1.00	3	64.66	831.67	1.66	458.40	1850.26	205.17
Ursus thibetanus	Ursidae	77.50	314.19	1.00	3	199.92	365.00	1.50	422.00	1015.00	82.01

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Viverra civettina	Viverridae				6						
Viverra megaspila	Viverridae	9.25	36.60	1.00							
Viverra tangalunga	Viverridae	8.68	24.05	1.00	6			1.92	144.00		
Viverra zibetha	Viverridae	9.50	36.97	1.00	6	80.30	182.50	2.89	240.00		
Viverricula indica	Viverridae	2.91	16.78	1.00	6			3.74	126.00		
Vormela peregusna	Mustelidae	0.54	4.76	1.00	1	60.83	365.00	5.07	107.00		
Vulpes bengalensis	Canidae	2.73	25.80	2.00	6	52.33	365.00	3.49	120.00		
Vulpes cana	Canidae				6	57.35		2.00	120.00	380.55	44.74
Vulpes chama	Canidae	2.96	33.50	2.00	6	52.59		2.50	120.00	311.36	
Vulpes corsac	Canidae				6	54.99	365.00	5.62		1024.89	54.56
Vulpes ferrilata	Canidae				1	54.23		3.49		420.91	55.68
Vulpes lagopus	Canidae	4.87	35.52	2.00	1	52.99	365.00	7.65	180.00	293.89	49.50
Vulpes macrotis	Canidae		30.76	2.00				4.50	240.00		
Vulpes pallida	Canidae	2.80	25.03	2.00	6			4.00	120.00		
Vulpes rueppellii	Canidae	3.25	24.29		1			2.12			
Vulpes velox	Canidae	2.20	32.14	1.50	1	53.70	365.00	4.25	240.00	470.29	47.08
Vulpes vulpes	Canidae	8.00	43.38	3.00	1	52.50	365.00	4.59	180.00	321.07	50.71
Vulpes zerda	Canidae	1.10	17.29	2.00	6	51.00	365.00	2.36	175.00	294.06	65.56
Zalophus californianus	Otariidae				6	349.99	547.50	1.41	360.00	2023.55	319.01